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1967 – 1968

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CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.

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Bulletin OF THE
Museum of
Comparative
Zoology

The Theridiid Spider Fauna of Chile

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 1
SEPTEMBER 29, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

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Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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THE THERIDIID SPIDER FAUNA OF CHILE

HERBERT W. LEVI

INTRODUCTION

Spiders are not good subjects for zoogeographic studies. The habit of ballooning practiced by members of many families facilitates wide distributions, sometimes continuous, sometimes scattered. It is therefore not surprising that many common spiders are found over most of Eurasia. Others, perhaps limited by climate or competition, occur only in the tropics or around the Mediterranean. A large number of spiders have become cosmopolitan, perhaps transported by man. In contrast, species of orthognath spiders (the mygalomorphs), scorpions, and wind scorpions (Solifugae) have limited distributions, and the American species of Solifugae represent families not found in Africa and Asia. Only one scorpion, *Isometrus maculatus* De Geer, is known to be pantropical. All others have restricted distributions, with geographical races that make study of their species difficult.

The theridiid spiders, the American representatives of which I have studied for the last 15 years, also have wide distributions and many are cosmopolitan. The great majority of species, at least in Europe, North and South America (outside Chile), belong to the genus *Theridion*. Some species of *Theridion* are also among the most common spiders. The genus *Theridion* is probably the second largest spider genus, after *Araneus*, with presumably several hundred species in the Americas.

It is therefore surprising that the theridiid spider fauna of Chile is completely different from that of the rest of the Americas and Eurasia. Only seven species of *Theridion*, all uncommon, are known from Chile. Most Chilean theridiid spiders, including most of the common ones, belong to the genus *Anelosimus*, which has more representatives in Chile than in the rest of the Americas. While the genera *Anelosimus*, *Episinus*, and *Styposis* are distinct in other areas studied, Chilean species of *Anelosimus* and the few *Episinus* species are probably closely related. In *Anelosimus attritus*, *A. episinoides* and *Episinus porteri*, the characteristics of pigmentation, shape of abdomen, and genitalia are intermediate between the two genera. *Episinus porteri* and *E. typicus*, unlike other members of their own genus, but like *Anelosimus*, have the lateral eyes close together. *Styposis selis* from southern Brazil has genitalia similar to those of Chilean *Anelosimus* species, and presumably other species of this rare genus will be found in the Southern Hemisphere.

Almost all Chilean theridiid spiders are endemic. The few that are not include *Paratheridula perniciosa* and species of the genus *Steatoda*. *Steatoda grossa* is cosmopolitan, and *S. ancorata* has a wide distribution in South America, where it prefers arid areas (as do two other species of *Steatoda*). Apparently, they have been able to invade Chile from the north. The cosmopolitan *Achaearanea tepidariorum* is found in cities. Even considering the effective isolation of Chile by deserts to the north, high mountains to the east, and an ocean to the west,

Figure 1. *Anelosimus roseus* (Nicolet), juvenile female. Abdomen with series of white spots on purple, sides greenish. (From Villarrica, Cautín Prov.; from color transparency.)

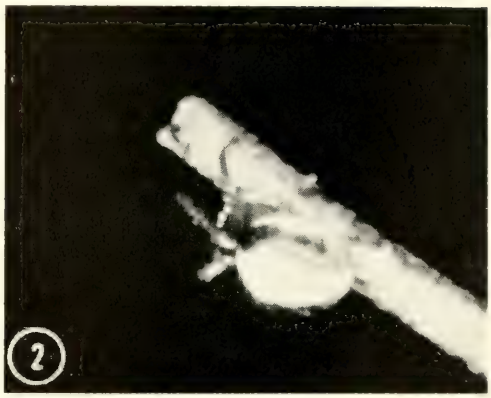


Figure 2. *Anelosimus roseus* (Nicolet), juvenile female. Abdomen with white band, sides purplish anteriorly, green posteriorly.

the amount of endemism is surprising. But from south central and southern Chile some theridiid species have penetrated into Argentina. Probably, these are species that can live in the forest that form a barrier to other species, but most *Anelosimus* do not seem to be forest dwellers and thus have not spilled eastward, and no representatives of the genera (for instance, *Theridion*) that one expects to be common in southern Argentina have invaded Chile. (But southern Argentine theridiids are not well known.)

The Chilean spider fauna strikes the visitor as being poor in number of species. Only a few species of Araneidae were collected; among the commonest in cities were *Zygiella x-notata* (Clerck) and *Araneus sericatus* Clerck imported from Europe. A *Zygiella x-notata* in the city park of Osorno had a 6 cm long dried lizard hanging in its web, which was attached to a concrete telephone pole! The two common species of *Argiope* are the cosmopolitan *A. trifasciata* and the tropical American *A. argentata*. In the areas in which I collected (except near the coasts) most crevices yielded only specimens of *Ariadna maxima* (Nicolet), in a habitat one might expect to harbor *Filistata*, araneids, agelenids, dictynids, and an occasional *Ariadna*.

Not only is the extreme endemism of species surprising, but so is the green or red color of many *Anelosimus* species and also of some species of Araneidae. Green is not a common color among spiders. (Unfortunately, the green readily washes out in alcohol, leaving the preserved specimens white, or white and gray.) The shade of green is variable, even in individuals of the same species from the same collecting site. (Though color photographs were taken of series collected at one site, the expense of reproducing them here is prohibitive.) Crude, unsuccessful attempts were made to learn whether species of *Anelosimus* and *Metabus* (Araneidae) will change their color with the background; there are indications, however, that the spiders select a site that matches their color. It was at first very difficult for me to find the habitats of the commonest *Anelosimus* species, my only clue being that they were collected by sweeping low vegetation. The cobwebs,

when finally found, were in tips of shrubs (Fig. 4), usually those having small leaves, the light green female under the leaf (Fig. 5), and the darker male along the stem in the same web.

Only a few collections were available from Juan Fernández Islands (all from one island, Más a Tierra), 650 km off the coast of Chile at the latitude of Santiago. The commonest species collected there is *Anelosimus roseus*, which is also the commonest species in Chile. Also included in the collection is one species of *Chrysso* and one of the *Theridion frondeum* group (*T. anson*), both species endemic to the island. Neither is known to have representatives in Chile. Of two additional new species from this island, one is close to *Anelosimus ocellatus* of Chile, the other close to *A. tepus*.

It is unfortunate that there exist no revisions of the spiders of Australia, South Africa, or as yet none of the theridiid spiders of New Zealand. The fauna of southern Argentina also is not well known, and only a few specimens from Argentina were at hand when I revised the American Theridiidae.

Some of the earliest collections and descriptions of American spiders were made by the Frenchman, Nicolet, in the lake area of Chile (Levi, 1964c). Shortly after the appearance of my paper on the history of 19th century South American spider studies, I received a letter regarding Nicolet from Dr. L. van der Hammen of Leiden. A part of his letter reads, "Nicolet must have been back in Paris already in 1846. In 1855 he published a paper entitled 'Histoire Naturelle des Acariens qui se trouvent aux environs de Paris.' In the introduction he writes 'en 1846 M. Milne Edwards m'ayant chargé . . .' Evidently he started his work in the Paris Museum at least in this year. Part of his types of South American spiders are apparently still present in Paris."

Although the South American theridiid spiders of the Paris Museum were made freely available to me by Prof. Vachon,

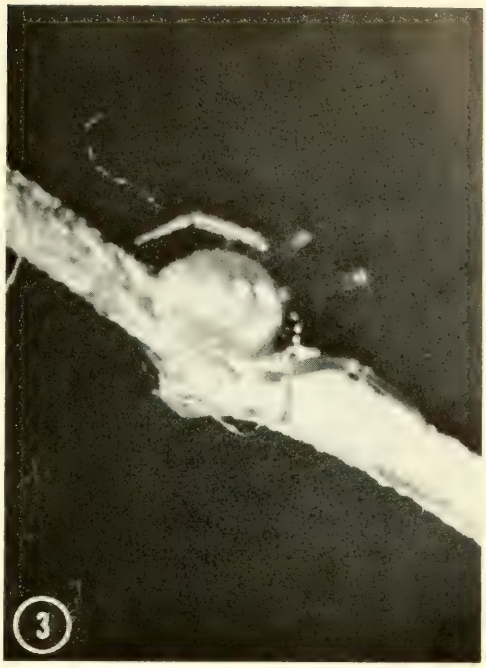


Figure 3. *Anelosimus roseus* (Nicolet), female. Abdomen with light red spots on bright red background. (Figures 2, 3 of specimens from Villarrica, Cautín Prov., from color transparencies taken with strobe flash.)

there were no specimens of Nicolet among them. After further search, a collection was found, only one vial of which had a label in Simon's handwriting. It appears that E. Simon, who published many papers on South American spiders, never examined the collection. However, not all of Nicolet's theridiid spiders were included in the newly found collection.

As a result of finding Nicolet's Chilean spider collection, there are some changes in names, emphasizing again the inadvisability of relying on early descriptions without reference to the types. The Nicolet species were based on color only, a variable character. The greens and reds rapidly wash out in alcohol; the white pigment is lost slowly. The Paris specimens, over 120 years in alcohol, are almost all colorless and in poor physical condition. An attempt has been made to determine the specimens and match them with recently collected

Figures 4, 5. *Anelosimus roseus* (Nicolet). 4. Web against sun. 5. Female spider, after plant was turned to get spider into sunshine. Spider with yellow median abdominal band, and red lateral bands. (Both from Petrohué; from color transparencies.)

ones, designating lectotypes where necessary.

In March 1965, I made a trip to Chile to collect and photograph in color the very interesting theridiid fauna—so distinct from the faunas of other parts of South America—and to collect with field data. I am grateful to my many friends and colleagues for their help, especially Mr. Luis Peña for advice on collecting sites, Prof. Patricio Sanchez of the Universita Católica of Santiago for his hospitality and advice, and to Prof. G. Mascetti, Mr. H. Perera L. and Señorita Joyce Allen of the Universidad Austral de Chile of Valdivia for going out of their way to help me in my collecting efforts. The research was supported in part by Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases.

As the spider fauna of Chile is distinct from that of the rest of America, this paper is published separately from one on South American theridiids.

A recent list of Chilean theridiid spiders was prepared, mainly from the literature, by Archer (1963). But as no illustrations or references to such accompany the text, the records were not used.

CATALOG OF CHILEAN THERIDIID SPIDERS

The areas of northern and southern limits of distribution are given.

Achaearanea chilensis Levi: Aconcagua

A. lota Levi: Concepción

A. teja sp. n.: Valdivia

A. tepidariorum (C. L. Koch): cosmopolitan, Taltal, Antofagasta, Santiago

Anelosimus attritus (Nicolet): Coquimbo to Llanquihue and Juan Fernández Islands

A. camoteensis sp. n.: Juan Fernández Islands

A. carelmapuensis Levi: Llanquihue to Magallanes

A. casablanca Levi: Coquimbo to Malleco

A. episinoides Levi: Linares

A. luisi sp. n.: Arauco to Tierra del Fuego

A. magallanes Levi: Osorno to Tierra del Fuego

A. michaelseni (Simon): Nuble to Magallanes

A. ocellatus (Nicolet), n. comb.: Cautín to Chiloé

A. osorno Levi: Osorno

A. portazuelo sp. n.: Juan Fernández Islands

A. purpureus (Nicolet), n. comb.: Coquimbo to Magallanes

A. roseus (Nicolet), n. comb.: Antofagasta to Chiloé, Juan Fernández Islands, the commonest theridiid in Chile and on Juan Fernández Islands

A. temuco Levi: Cautín

A. tepus sp. n.: Osorno

A. ventrosus (Nicolet), n. comb.: Arauco to Tierra del Fuego

A. wellingtoni sp. n.: Magallanes

Argyrodes elevatus Taczanowski: Coquimbo

Chrysso backstromi (Berland): Juan Fernández Islands

Dipoena chillana Levi: Linares to Nuble

D. ohigginsi Levi: O'Higgins

Enoplognatha zapfeae Levi: Tarapacá

Episinus porteri (Simon), n. comb.: Cautín to Tierra del Fuego

E. typicus (Nicolet): Arauco to Chiloé

Latrodectus sp. The species once was erroneously thought to be *L. curacaviensis* (Müller). It is not known whether this species is the same one found in northern Argentina or is endemic. It is possible that *L. mactans* (Fabricius) occurs in Chile; much work must be done on the difficult but medically important species of *Latrodectus* before we will know. Specimens come from the provinces of Valdivia and Santiago, others as far south as the Straits of Magallan.

Paratheridula perniciosa (Keyserling):

Figures 6, 7. *Anelosimus ocellatus* (Nicolet). Females. 6. Color of spider green with a red mark on each side of abdomen. 7. Color of spider green with a white band on each side of abdomen. (Petrohué; to obtain sufficient light for ph:tographing, the plant was turned; from color transparencies.)

southern United States to Chile and probably Argentina

Phoroncidia coquimbo Levi: Coquimbo

P. margamarga Levi: Valparaiso to Osorno

P. puyehue sp. n.: Osorno

P. scutula (Nicolet): Bolivia to Aysen

Steatoda ancorata (Holmberg): Mexico to southern Argentina and southern Chile

S. andina (Keyserling): Ecuador to Tarapacá

S. grossa (C. L. Koch): cosmopolitan, Antofagasta to Osorno

S. porteri (Simon): Atacama to Coquimbo

S. sabulosa (Tullgren): Bolivia to Magallanes, southern Argentina

Theridion agreste Nicolet: Coquimbo to Magallanes

T. albolineatum Nicolet: Valdivia

T. amarga sp. n.: Linares to Magallanes; Santa Cruz, Argentina

T. ambiguum Nicolet: Concepión to Llanquihue

T. anson sp. n.: Juan Fernández Islands

T. albolineatum Nicolet: Valdivia

T. funerarium Nicolet: This may be *Coleosoma floridanum* Banks.

T. linaresense Levi: Santiago to Linares

Erroneous record: *Helvibis chilensis* (Keyserling, 1884) probably comes from the upper Amazon Basin, where a male matching the female type has been found. All other species of *Helvibis* come from the Amazon region.

KEY TO GENERA OF THERIDIID SPIDERS OCCURRING IN CHILE

For determining species, it will be necessary to refer to the keys and illustrations in my revisions of American Theridiidae listed in the references. Names that had to be changed as a result of the discovery of the Nicolet collection are discussed below.

1a. Abdomen heavily sclerotized, with plates (Figs. 21, 26) ..... *Phoroncidia*
1b. Abdomen soft 2
2a. Fleshy colulus between anterior spinnerets (*Anelosimus ventrosus, Enoplognatha, Latrodectus, Steatoda*) 3
2b. No colulus or two setae between anterior spinnerets 7
3a. Chelicerae without teeth ..... *Latrodectus*
3b. Chelicerae with teeth 4
4a. Abdomen ovoid, eye region of male without projections 5
4b. Abdomen drawn out beyond spinnerets or high; eye region of male with projections ..... *Argyrodes*
5a. Chelicerae with teeth on anterior margin only ..... *Steatoda*
5b. Chelicerae with teeth on anterior and posterior margin 6
6a. Chelicerae with a blunt small tooth on posterior margin ..... *Enoplognatha*
6b. Chelicerae with a row of small teeth on posterior margin ..... *Anelosimus ventrosus, A. wellingtoni*
7a. No setae between anterior spinnerets (*Achaearanea, Chrysso, Paratheridula, Theridion*) 8
7b. Two setae between anterior spinnerets 11
8a. Abdomen higher than long, with streaks down sides ..... *Achaearanea*
8b. Abdomen longer than wide or high 9
9a. Abdomen with a dorsal posterior hump; from Juan Fernández Islands only ..... *Chrysso*
9b. Abdomen without dorsal posterior hump 10
10a. One tooth on posterior margin of chelicerae ..... *Paratheridula*
10b. No teeth on posterior margin ..... *Theridion*
11a. Abdomen pear-shaped or with humps much longer than wide (Fig. 39) ..... *Episinus*
11b. Abdomen oval; or if with humps (*Anelosimus attritus, A. episinoides*), abdomen as wide or wider than long 12
12a. Chelicerae with a posterior row of small teeth, females usually with one pair of seminal receptacles ..... *Anelosimus*
12b. Chelicerae without teeth on posterior margin, females with two pairs of seminal receptacles ..... *Dipoena*

COMMENTS ON INDIVIDUAL SPECIES

Paratheridula perniciosa (Keyserling)

Paratheridula quadrimaculata, —Levi, 1957: 106, figs. 1–6, ♀ ♂, map.

This tiny species has been collected in Osorno Province: 18 km west of Purranque, 10 km east of Puyehue, both by E. S. Ross and A. E. Schlinger in January 1951.

It is believed to live under rocks in fields and parks.

Achaearanea tepidariorum (C. L. Koch)

Achaearanea tepidariorum, —Levi, 1955: 32, figs. 69–70, 83–84, ♀ ♂; 1963c: 215, map 1.

This cosmopolitan species, which may

be native to Peru, is known from Taltal, Antofagasta, Santiago. Individuals were collected on buildings in Villarrica, Cautín.

Achaearanea teja sp. n.
Figures 8–10

Holotype. Female from Isla Teja, Valdivia, Prov. Valdivia, on farmland, 6 March 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the type locality.

Description. Carapace and sternum dark brown. Legs yellow-white with dark brown rings. Abdomen has the lateral black and white stripes characteristic of many species of the genus. There is a median dorsal longitudinal dark mark and one or two pairs of white spots on the venter. Anterior median eyes slightly smaller than others, one and one-half diameters apart, almost touching laterals. Posterior median eyes one diameter apart, a little less than one diameter from laterals. Abdomen higher than long, with a median tubercle. Total length, 2.5 mm. Carapace, 1.0 mm wide, 1.1 mm long. First femur, 1.7 mm; patella and tibia, 1.6 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm. Second patella and tibia, 1.1 mm; third, 0.8 mm; fourth, 1.3 mm.

Diagnosis. Achaearanea teja differs from *A. leguiai* (Chamberlin), found in Peru, by being smaller, and by the epigynum (Fig. 10), the sclerotized plate of which is wider than long, while in *A. leguiai* it is longer than wide.

Records. Three ♀ paratypes collected with holotype, one deposited in the American Museum of Natural History.

Theridion agreste Nicolet

Theridion agreste Nicolet, 1849: 540. Female lectotype here designated and juv. ♀, ♂ paralectotypes, from Janquique [Llanquihue], Chile, are in the Muséum National d'Histoire Naturelle, Paris; examined.

Theridion ambiguum, —Levi, 1963d: 538, figs. 54–58, ♀ ♂. Not *T. ambiguum* Nicolet.

Additional record. Coquimbo: Llapel, Caimanes (H. Zapfe de Mann).

Theridion ambiguum Nicolet

Theridion ambiguum Nicolet, 1849: 532. Three female syntypes from Valdivia, Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. Not *T. ambiguum*, —Levi, 1963d.

Theridion penai Levi, 1963d: 537, figs. 52, 53 ♀. Female holotype from Maullín Llanquihue, Chile, in the Institut Royal des Sciences Naturelles de Belgique, Brussels. NEW SYNONYMY.

Theridion albolineatum Nicolet
Figures 14–15

Theridion albolineatum Nicolet, 1849: 533. Female lectotype here designated from Valdivia, Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. Not *Anelosimus albolineatus*, —Levi, 1963a.

Description. Nicolet's specimens, after 130 years in alcohol, lack coloration. The anterior median eyes are slightly smaller than the others, two diameters apart, one diameter from laterals. Posterior eyes are one and one-quarter diameters apart. The abdomen is spherical. Total length 4.2 mm. Carapace 1.3 mm long, 1.2 mm wide. First patella and tibia, 2.0 mm; second, 1.5 mm; third, 1.1 mm. Fourth femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. The indistinct epigynum (Fig. 15) has two dark spots with seminal receptacles showing through the integument anteriorly.

Record. One paralectotype originally in the same vial as the lectotype.

Theridion linaresense Levi

Theridion linaresense Levi, 1963d: 537, figs. 50–51. Female holotype from Linares, Linares Prov., Chile, in the Institut Royal des Sciences Naturelles de Belgique, Brussels.

Record: *Santiago*: Caracaví, 30 September 1964, ♀ ♀ (H. Zapfe de Mann).

Theridion amarga sp. n.

Theridion foliaceum, —Levi, 1963d: 536, figs. 44–46, ♀ ♂. Not *T. foliaceum* Nicolet.

Holotype. Female from Laguna Amarga, Natales, Magallanes, Chile, 14–21 Dec. 1960 (L. Peña), in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the type locality.

Theridion anson sp. n.
Figures 11–13

Holotype. Male from Plazoleto de Yunque, Valle Anson, 200–250 m, Isla Más a Tierra, Juan Fernández Islands, 1–28 April 1962 (B. Malkin), in the American Museum of Natural History. The specific name is a noun in apposition, after the type locality.

Description. The spider is yellow-white except for the black eye region and clypeus and a wide black median dorsal band and a wide black margin around the carapace. The legs are yellow-white with the distal ends of the femora and tibiae black, darker on venter. The dorsum of the abdomen has white pigment spots, the sides have some black pigment spots, and there is a transverse band of black spots. Anterior median eves smaller than others, one and one-half diameters apart, two diameters from laterals. Posterior median eyes one diameter apart, two diameters from laterals. Abdomen quite long. Total length 2.9 mm. Carapace, 1.3 mm long, 1.1 mm wide. First femur, 3.2 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm; fourth, 1.9 mm.

Diagnosis. This species, which belongs to the *Theridion frondeum* group, can be differentiated from others by the very long femur of the palpus, 0.8 mm long, and by the very long endites of the palpal coxae (Fig. 13). Also the palpus (Figs. 11, 12) is distinct.

Habits. The long legs suggest that, unlike other *Theridion* species found in Chile, this species lives in vegetation rather than under stones.

Records. Fragments of a male paratype collected with holotype.

Chrysso backstromi (Berland)

Theridion bäckströmi Berland, 1924: 426, figs. 4–6 ♀. Female holotype from Juan Fernández Islands, in the Natural History Museum, Stockholm.

Chrysso backstromi, —Levi, 1962b: 230, figs. 58–60, ♀.

This species, previously known only from the holotype, is variable, as are Chilean *Anelosimus*. Of the specimens on hand, no two have the same distribution of black and white pigment, and in some the black pigment pattern on the abdomen resembles that of *Episinus*. It would be interesting to know whether it is brightly colored in life.

Record. Juan Fernández Islands: Isla Más a Tierra, Valle Anson, 200–250 m, April 1962 (B. Malkin).

Anelosimus roseus (Nicolet) new combination
Figures 1–5

Theridion roseum Nicolet, 1849: 527. Female syntypes from Valdivia, Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.

Theridion rubicundum Nicolet, 1849: 530. Male lectotype here designated, female paralectotypes, from Valdivia, Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY.

Theridion bucculentum Nicolet, 1849: 531. Two males, one female, syntypes from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY. Not *Anelosimus bucculentus*, —Levi, 1963a.

Theridion opimum Nicolet, 1849: 534. Female holotype from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY.

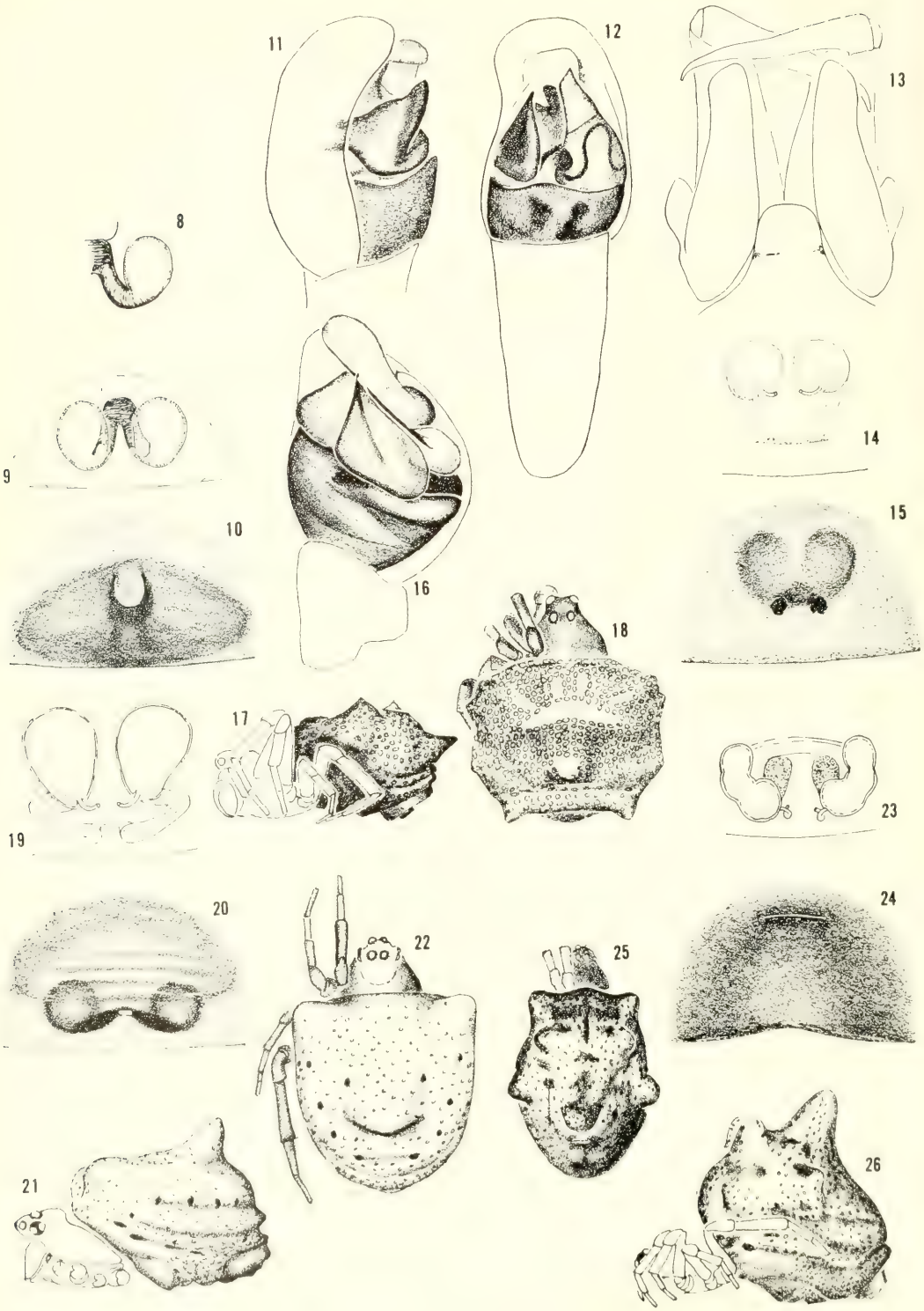
Theridion foliaceum Nicolet, 1849: 538. Female syntypes from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY. Not *Theridion foliaceum*, —Levi, 1963d.

Theridion gracile Keyserling, 1884: 32, pl. 2, fig. 16, ♀. Female lectotype from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY.

Anelosimus gracilus, —Levi, 1963a: 37, figs. 5–13, ♀ ♂.

This is the commonest Chilean theridiid species, also common on Juan Fernández Islands. It is collected by sweeping low shrubs. At the tips of the shrubs it makes a fine cobweb, about 50 cm to 1 m from the ground (Fig. 4). The male tends to sit along the stem, the female under a leaf or in a leaf axil in the same web (Fig. 5). One egg sac, photographed, seemed to be attached to the substrate, while in other *Anelosimus* species observed, the female was seen to carry the egg sac or suspend it in a web.

The abdomen of the male is bright red to purplish red; that of the female may be bright green. Often the female has a wide median pigment stripe (Figs. 2, 5), with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the sides bright green, or bright red to brown. No two specimens, even of those collected together, were the same color, an observation that is supported by the color photographs (Figs. 1–3). As far as is known, this species occurs from Antofagasta Province to Chiloé.

Anelosimus purpureus (Nicolet), new combination

Theridion purpureum Nicolet, 1849: 529. Female lectotype here designated, from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.

Theridion transversum Nicolet, 1849: 529. Several specimens that may have been Nicolet's are in the Muséum National d'Histoire Naturelle, Paris. They have a label written by E. Simon and the number 3426. The specimens came from Valdivia, as do the types. Presumably Simon wrote a new label and discarded the original one. NEW SYNONYMY.

Anelosimus bucculentus, —Levi, 1963a: 41, figs. 27–30, ♀, ♂. Not *T. bucculentum* Nicolet.

The sides of the dorsum of the abdomen of a recently collected female are purple, the middle gray, the sides gray. There is a white spot on the dorsum some distance from the spinnerets. Another specimen had the sides of the carapace orange, the center brown and a black V between. The sternum was orange. The abdomen had a wide, longitudinal, median black band; on the sides, a white line and purple between the black and white. On the sides of the white line was some black pigment; the legs and venter were yellow-white. The species is known from Coquimbo Province south to Magallanes.

Additional records. Llanquihue: Ensenada, in low vegetation of beach of Lago Llanquihue, ♀; Petrohué, 200 m, in low vegetation. *Magallanes*: Puerto Edén, *ca.* 49°S, Wellington Isl. Dec. 1962, ♀ (P. J. Darlington).

Anelosimus ocellatus (Nicolet), new combination

Figures 6, 7, 27

Theridion ocellatum Nicolet, 1849: 532. Female lectotype here designated, from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.

Theridion viride Nicolet, 1849: 536. Female lectotype, one female paralectotype here designated, from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined (a male paralectotype is *A. michaelseni* Simon). NEW SYNONYMY. Not *T. viride* Wider, 1832.

Theridion virgulatum Nicolet, 1849: 537. No specimens so labelled, but specimens labelled *Theridion variegatum* Nicolet. Holotype from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY. Not *T. variegatum* Brullé, 1832.

Theridion viridulum Roewer, 1942: 500. New name for *T. viride* preoccupied.

Anelosimus chiloensis Levi, 1963a: 41, figs. 25, 26, ♀. Female holotype from Chaitén, Chiloé, Chile (L. Peña), in the Institut Royal des Sciences Naturelles de Belgique, Brussels. NEW SYNONYMY.

Description. Male. Carapace light brown. Abdomen with a median white band and a black spot posteriorly on dorsum. All eyes very small, anterior medians smallest. Posterior median eyes slightly oval with the long diameter lying in anteroposterior direction. Anterior median eyes less than two diameters apart, one and one-half from laterals. Posterior eyes two (short) diameters apart. Total length, 2.7 mm. Carapace, 1.3 mm long, 0.9 mm wide. First femur, 2.4 mm; patella and tibia, 2.9 mm; metatarsus, 1.5 mm; tarsus, 0.8 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.3 mm.

Diagnosis. This species is difficult to

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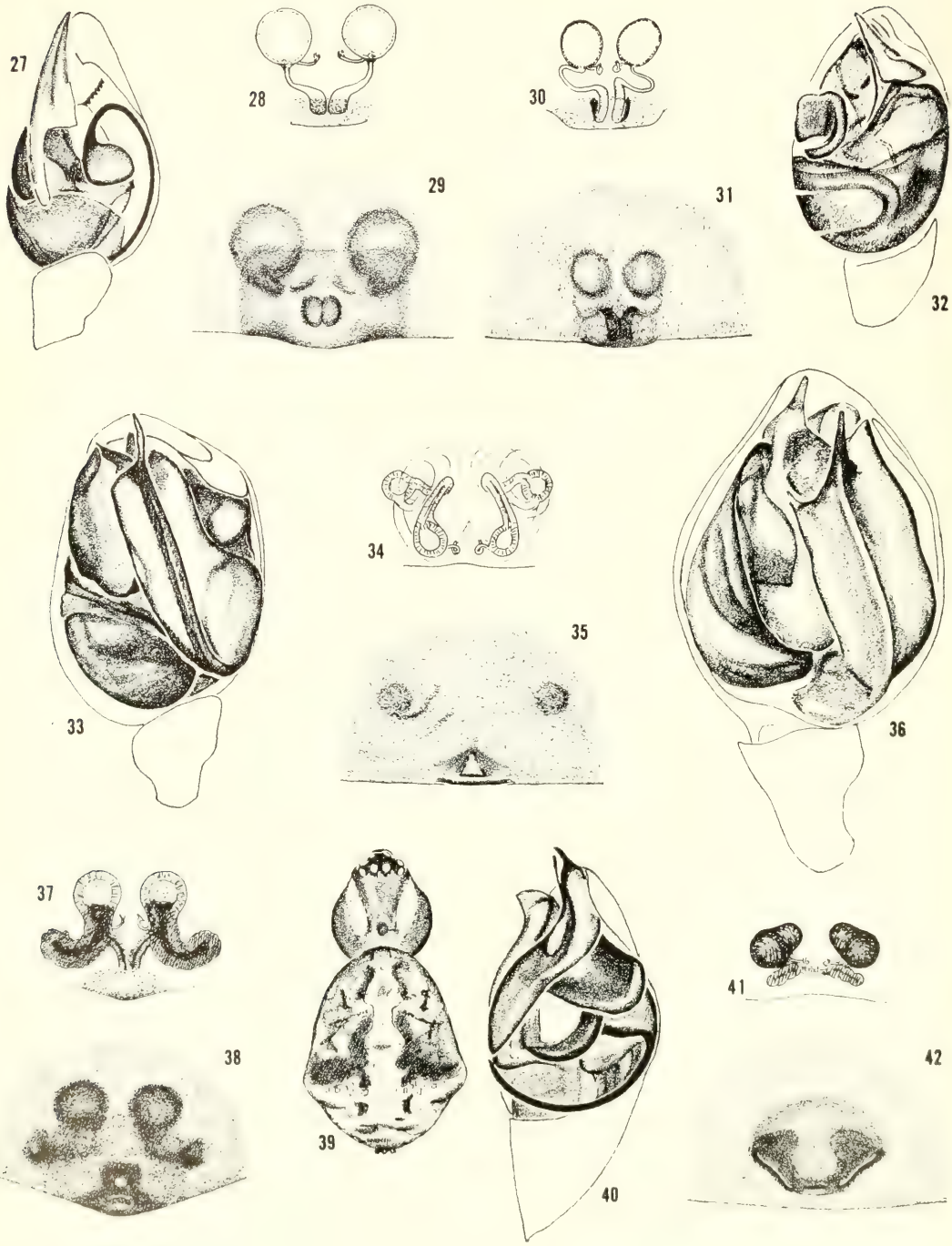
Figures 8–10. *Achaearanea teja* sp. n. 8, 9. Female genitalia. 8. Mesal view. 9. Dorsal view. 10. Epigynum.
Figures 11–13. *Theridion anson* sp. n. 11, 12. Left palpus. 11. Ectal view. 12. Ventral view. 13. Labium, endites of palpal coxae and chelicerae in ventral view.
Figures 14–15. *Theridion albolineatum* Nicolet. 14. Female genitalia, dorsal view. 15. Epigynum.
Figures 16–18. *Phoroncidia margamarga* Levi. 16. Left palpus, ventral view. 17, 18. Male.
Figures 19–22. *Phoroncidia scutula* (Nicolet). 19. Female genitalia, dorsal view. 20. Epigynum. 21–22. Female.
Figures 23–26. *Phoroncidia puyehue* sp. n. 23. Female genitalia, dorsal view. 24. Epigynum. 25–26. Female.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identify. The epigyna are lightly sclerotized and variable among individuals. The living animals, light green with white or red spots, are found under leaves of herbaceous plants (Figs. 6, 7). The green washes out almost immediately in alcohol. The males and females were not collected together and there remains slight doubt that they belong together.

Records: *Cautín*: Villarrica ♀. *Valdivia*: Valdivia ♂. *Osorno*: Termas de Puyehue ♀. *Llanquihue*: Petrohué ♀; Peulla ♂.

Anelosimus luisi sp. n.

Anelosimus albolineatus, —Levi, 1963a: 42, figs. 35–38, ♀ ♂. Not *Theridion albolineatus* Nicolet.

Holotype: Female from Camerón, Tierra del Fuego, Magallanes, Chile, 14 Nov. 1960 (L. Peña), in the Museum of Comparative Zoology. The species is named after its collector, Luis Peña.

Distribution. Chile from Province Arauco to Tierra del Fuego.

Anelosimus carelmapuensis Levi
Figure 33

Anelosimus carelmapuensis Levi, 1963a: 45, figs. 45–48, ♀. Female holotype from Carelmapu, Llanquihue, Chile, in the Institut Royal des Sciences Naturelles de Belgique, Brussels.

This species has been known only from the type specimen.

Description. Male. Carapace yellow with a gray band as wide as eye region in front, narrowing on thorax; black rings around eyes. Legs light brown with indistinct lighter rings. Abdomen light on each side, with gray and white spots on dorsum, black patch above spinnerets. Posterior median eyes wider than long, anterior median eyes smallest. Anterior median eyes one diameter apart, one diameter from laterals. Total length, 2.7 mm. Carapace, 1.3 mm long, 1.1 mm wide. First femur, 2.5 mm; patella and tibia, 2.8 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 1.7 mm; third, 1.2 mm; fourth, 1.3 mm.

Additional record. Magallanes: Puerto Edén, *ca.* 49° S. Wellington Island, Dec. 1962, ♀ (P. J. Darlington); 10–13 Dec. 1962, ♂; 13–15 Dec. 1962, ♂ (P. J. Darlington).

Anelosimus magallanes Levi

Anelosimus magallanes Levi, 1963a: 42, figs. 31–34, ♀ ♂. Male holotype from Camerón, Tierra del Fuego, Magallanes, Chile, in the Museum of Comparative Zoology.

After one year in alcohol the carapace is brown in the middle. The dorsum of the abdomen has a broad transverse band made up of white pigment spots, that divides the abdomen into equal thirds. The anterior third is black with a purple area posteriorly on each side toward the white band; the area posterior of the white band is purple. All other parts are yellow-white.

Additional record. Osorno: Termas de Puyehue, 240 m, 14 March 1965, ♀.

Anelosimus ventrosus (Nicolet), new combination

Theridion ventrosum Nicolet, 1849: 536. Female lectotype here designated, from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.

Theridion recurvatum Tullgren, 1901: 191. Female holotype from Patagonia, in the Natural History Museum, Stockholm; examined. NEW SYNONYMY.

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Figures 27. *Anelosimus ocellatus* (Nicolet), left palpus.
Figures 28–29. *Anelosimus tepus* sp. n. 28. Female genitalia, dorsal view. 29. Epigynum.
Figures 30–32. *Anelosimus camoteensis* sp. n. 30. Female genitalia, dorsal view. 31. Epigynum. 32. Left palpus.
Figure 33. *Anelosimus carelmapuensis* Levi, left palpus.
Figures 34–36. *Anelosimus portazuelo* sp. n. 34. Female genitalia, dorsal view. 35. Epigynum. 36. Left palpus.
Figures 37–38. *Anelosimus wellingtoni* sp. n. 37. Female genitalia, dorsal view. 38. Epigynum.
Figures 39–42. *Episinus porteri* (Simon). 39. Female. 40. Left palpus. 41. Female genitalia, dorsal view. 42. Epigynum.

Anelosimus recurvatus, —Levi, 1963a: 45, figs. 49–52, ♀ ♂.

Note. One female marked *T. ventrosum* from the Chilean Nicolet collection is *Enoplognatha ovata* (Clerck) of Europe. This species is not known to have been transplanted to Chile.

Anelosimus michaelseni (Simon)

Theridion michaelseni Simon, 1902: 14. Female holotype from Tierra del Fuego, in the Muséum National d'Histoire Naturelle, Paris; examined.
Anelosimus michaelseni, —Levi, 1963a: 44, figs. 41–44, ♀ ♂, map.

Additional record. Llanquihue: Petrohué, 200 m, in low shrubs, 20 March 1965, ♂.

Anelosimus portazuelo sp. n.
Figures 34–36

Holotype. Female from Portazuelo trail, Isla Más a Tierra, Juan Fernández Islands, 7 April 1962 (B. Malkin), in the American Museum of Natural History. The specific name is a noun in apposition, after the type locality.

Description. In alcohol, the specimens are completely yellow-white, with some white pigment spots on dorsum of abdomen. (In some specimens, there are white spots around the sides.) Eyes of female are small and equal in size. Anterior median eyes two diameters apart, three diameters from laterals. Posterior eyes three diameters apart. Chelicerae with three teeth on anterior margin, four denticles on posterior margin. Abdomen suboval. Total length, 2.7 mm. Carapace, 1.1 mm long, 1.1 mm wide. First femur, 1.9 mm; patella and tibia, 1.6 mm; metatarsus, 1.5 mm; tarsus, 0.8 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm; fourth, 1.1 mm.

Male has anterior median eyes smaller than others, two diameters apart and more than three diameters from laterals. Posterior median eyes two and one-half diameters apart, three diameters from laterals. Total length, 2.5 mm. Carapace, 1.3 mm long, 1.3 mm wide. First femur, 2.5 mm; patella and tibia, 3.2 mm; metatarsus, 2.7 mm; tarsus, 0.9 mm. Second patella and tibia, 1.7 mm; fourth, 1.5 mm.

Diagnosis. Only the genitalia (Figs. 34–36) separate this small-eyed *Anelosimus* from *A. ocellatus*. Unlike all other species the female has two pairs of seminal receptacles of variable distance from each other (Fig. 34). The epigynum is an indistinct structure.

Records. Juan Fernández Islands: Isla Más a Tierra, paratype collected with female; paratypes from El Camote, 600–650 m, ♀; Plazoleto de Yunque, 200–250 m, ♂; Quebrada Demajuana, 3 ♂ (all April 1962, B. Malkin).

Anelosimus wellingtoni sp. n.
Figures 37–38

Holotype. Female from Puerto Edén, 49° S, Wellington Island, Magallanes, Chile, 7–9 Dec. 1962 (P. J. Darlington), in the Museum of Comparative Zoology. The species, like the island of the type locality, is named after the Duke of Wellington.

Description. Carapace yellowish with a brown band as wide as posterior median eyes in front, narrowing behind. Legs yellowish. Dorsum of abdomen with a purplish brown pattern of large spots; a single anterior spot with three posteriorly directed branches, and two spots on each side, the posterior pair of which join medially, and posteriorly fuse with a median stripe toward the spinnerets. Venter and sides of venter of abdomen brownish except for epigastric area, which is light. Anterior median eyes slightly smaller than others, one diameter apart, one diameter from laterals. Posterior median eyes one diameter apart, one diameter from laterals. The colulus is large and has two setae on its sides. Total length, 3.5 mm. Carapace, 1.5 mm long, 1.4 mm wide. First femur, 2.4 mm; patella and tibia, 2.4 mm; metatarsus, 1.9 mm; tarsus, 1.1 mm. Second patella and tibia, 1.8 mm; third, 1.4 mm; fourth, 2.0 mm.

Diagnosis. This species is similar to *Anelosimus ventrosus* and *A. carelmapuensis*, but has the fused ducts curved anterolater-

ally (Fig. 37), and the opening of the epigynum has a different shape (Fig. 38).

Anelosimus attritus (Nicolet)

Theridion attritum Nicolet, 1849: 541. Female holotype from Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.
Conopistha barrosi Mello-Leitão, 1951: 330, fig. 2. Female holotype from Maullín, Chile, in the Museu Nacional, Rio de Janeiro; examined.
Anelosimus attritus, —Levi, 1963a: 38, figs. 14–19, ♀, ♂.

The living spiders lack bright colors; they have a black or gray pattern on yellow-white or white, quite variable. The species is easily recognized by the shape of its abdomen, subtriangular and wider than long. Color photographs were taken.

Additional records. Cautín: Villarrica. *Osorno*: Termas de Puyehue. *Llanquihue*: 2–3 km NW of Ensenada.

Anelosimus tepus sp. n.
Figures 28–29

Holotype. Female from Termas de Puyehue, Osorno, Chile, 240 m, 14 March 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. In alcohol, carapace dark yellow with black rings around eyes. Sternum and legs, dark yellow. Abdomen uniformly light gray with scattered black pigment. Median eyes smaller than laterals, anterior medians the smallest. Anterior median eyes one and one-half diameters apart, one diameter from laterals. Posterior median eyes less than one diameter apart, one diameter from laterals. Total length, 2.2 mm. Carapace, 0.92 mm long, 0.80 mm wide. First femur, 1.09 mm; patella and tibia, 1.30 mm; metatarsus, 0.84 mm; tarsus, 0.63 mm. Second patella and tibia, 1.05 mm; third, 0.83 mm; fourth, 1.20 mm.

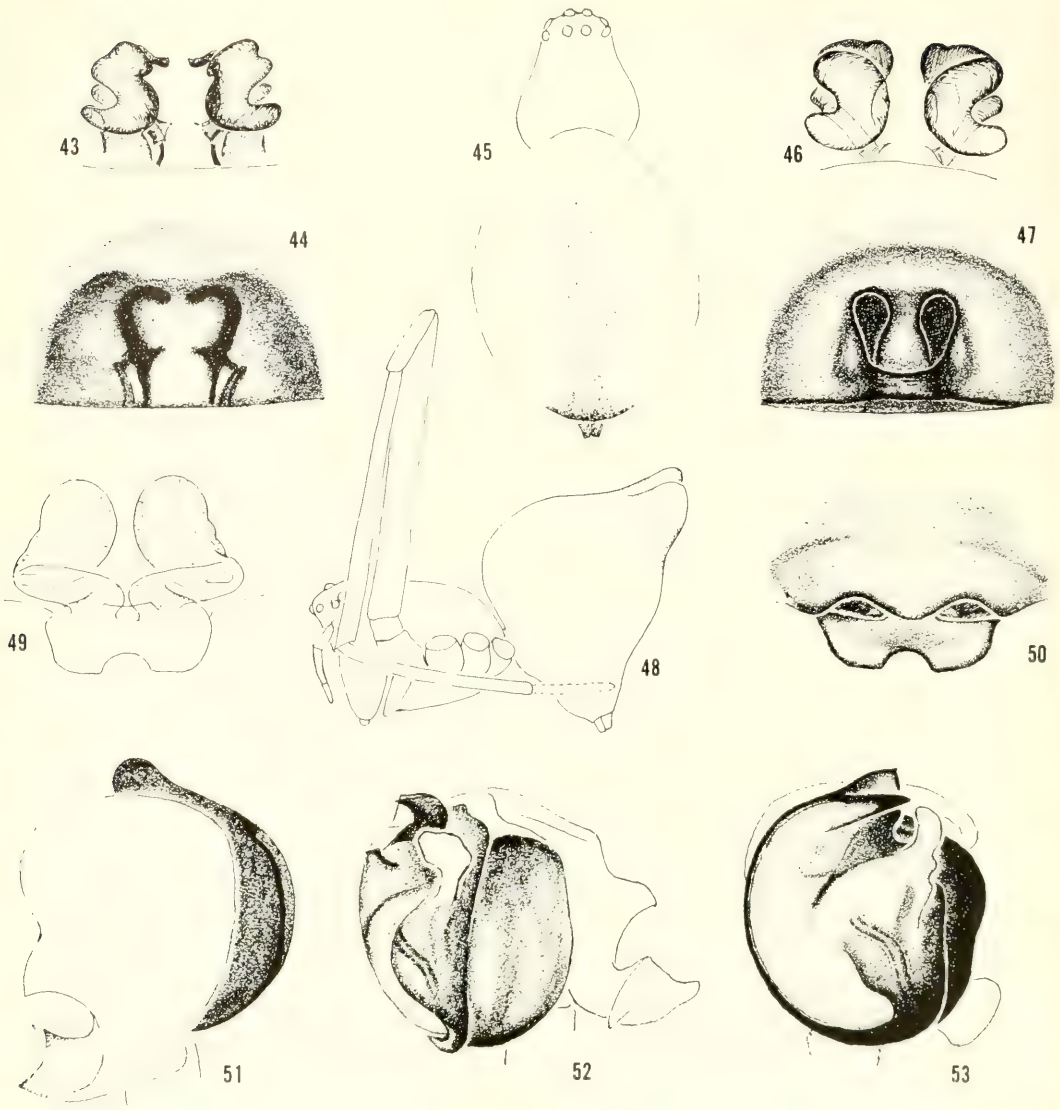
Diagnosis. This species is readily separated from most other *Anelosimus* by the unusual coloration and by the epigynum, which is a transparent plate; the openings are two dark median oval spots (Fig. 29). The epigynum is similar to that of *Anelosimus camoteensis* but the ducts are shorter (Fig. 28).

Anelosimus camoteensis sp. n.
Figures 30–32

Holotype. Female from Isla Más a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m, Camote side, Juan Fernández Islands, 1–28 April 1962 (B. Malkin), in the American Museum of Natural History. The specific name is an adjective, after Camote, where specimens have been collected.

Description. Carapace yellow-white with a black band as wide as the eye region covering almost the whole carapace. Legs yellow-white with ends of segments darker. Abdomen with white and black pigment spots on dorsum. Venter almost without pigment or two white spots side by side. Anterior median eyes smaller than others, their diameter apart, and less than one diameter from laterals. Posterior median eyes two-thirds their diameter apart, their radius from laterals. Chelicerae with a keel as wide as long on the posterior border. Abdomen of male higher than that of female, otherwise sexes much alike. Female, total length, 1.5 mm. Carapace, 0.6 mm long, 0.5 mm wide. First femur, 0.8 mm; patella and tibia, 0.9 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 0.6 mm; third, 0.5 mm; fourth, 0.6 mm. Male, total length, 1.2 mm. Carapace, 0.6 mm long, 0.5 mm wide. First femur, 0.9 mm; patella and tibia, 0.9 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm. Second patella and tibia, 0.6 mm; third, 0.5 mm; fourth, 0.6 mm.

Diagnosis. This very small, large-eyed species resembles species of *Mysmena*. The two setae seem to be on a very short colulus. The epigynum (Fig. 31) is variable and asymmetrical in the one specimen dissected (Fig. 30). The palpus (Fig. 32), except for a mesal sclerite, is lightly sclerotized and unlike that of any other *Anelosimus* species except the larger *A. tepus*. The connecting ducts of the female of *A.*



Figures 43–44. *Ceratinopsis distincta* (Nicolet). 43. Female genitalia, dorsal view. 44. Epigynum. Figures 45–47. "*Ceratinopsis*" *modesta* (Nicolet). 45. Female. 46. Female genitalia, dorsal view. 47. Epigynum. Figures 48–53. *Ero spinipes* (Nicolet). 48. Juvenile lectotype. 49. Female genitalia, dorsal view. 50. Epigynum. 51–53. Left palpus. 51. Dorsal view. 52. Ectal view. 53. Ventral view.

camotecnsis (Fig. 30) are longer. The coloration appears to be variable.

Records. Juan Fernández Islands: Isla Más a Tierra, ♂ paratype collected with ♀ holotype; El Camote, 600 m, 19 April 1962, 2 ♀ (B. Malkin); Valle Villagra, Portazuelo trail, 400–450 m, 19 April 1962, ♂ paratype (B. Malkin).

Episinus porteri (Simon), new combination
Figures 39–42

Chrosiothes australis Simon, 1896: 143. Female

holotype from Tierra del Fuego [Argentina], in the Muséum National d'Histoire Naturelle, Paris; examined. Not *Episinus australis* Keyserling, 1890.

Chrosiothes porteri Simon, 1901: 18. Holotype from western Patagonia, probably lost or in vials with *C. australis* types.

Theridium spinatum Tullgren, 1901: 189, pl. 15, fig. 2, ♀♂. Female and male syntypes from Patagonia, in the Natural History Museum, Stockholm; examined.

?*Theridium fuegianum* Simon, 1904: 90. Juvenile holotype from Allen Gardiner, Tierra del Fuego, Chile, in the Muséum National d'Histoire Naturelle, Paris; examined.

Anelosimus australus, —Levi, 1963a: 47, figs. 53–57.

Note. At the time I wrote my 1963 paper I had examined only the types as no other specimens were available.

Description. Female. Carapace light gray with lighter V-shaped mark. Eyes in a dark, almost black area. Abdomen heavily marked by black pigment, with only very little scattered white pigment (Fig. 39). There is a median light stripe, and humps are black anteriorly, yellow-white posteriorly. Carapace has a central depression. Anterior median eyes smaller than others. Anterior median eyes one-third their diameter apart, one-third from laterals. Posterior median eyes one diameter apart, one-third diameter from laterals. Abdomen of female has one pair of humps at the middle. Total length, 3.8 mm. Carapace 1.3 mm long, 1.3 mm wide. First femur, 2.1 mm; patella and tibia, 2.5 mm; metatarsus, 1.8 mm; tarsus, 1.0 mm. Second patella and tibia, 1.6 mm; third, 1.3 mm; fourth, 2.1 mm.

Male. Markings as in female, but abdomen lacks the humps. Anteriorly, the two black patches on each side are broken by a median longitudinal band which meets a transverse band at about the middle; posterior with pigment. Male, total length, 2.5 mm. Carapace, 1.1 mm long, 1.0 mm wide. First femur, 2.3 mm; patella and tibia, 2.7 mm; metatarsus, 2.2 mm; tarsus, 1.0 mm. Second patella and tibia, 1.5 mm; third, 1.1 mm; fourth, 1.8 mm.

Diagnosis. The epigynum (Fig. 42) has two heavily sclerotized diagonal slits, closer to each other posteriorly. The epigynum and palpus (Figs. 40–42) distinguish the species readily from *Episinus typicus*.

Records. Cautín: Villarrica, forest, 3–4 March 1965, ♀. *Llanquihue*: Peulla, 200 m, marsh and cliff, 24 March 1965, ♂.

Episinus typicus (Nicolet)

Theridion typicum Nicolet, 1849: 539. Male lectotype here designated, two female paralectotypes, in the Muséum National d'Histoire Naturelle, Paris; examined.

Episinus typicus, —Levi, 1964a: 10, figs. 12–15, ♀, ♂.

Note. One female paralectotype is a linyphiid.

Description. The specimens do not change color in alcohol. They are mottled gray and black, very variable.

Habits. Almost all specimens collected were swept from vegetation in forests, a few from shaded habitats. In March, all specimens collected were mature males and females.

Additional records: *Osorno*: Termas de Puyehue, forest. *Llanquihue*: Ensenada, 50 m, shaded roadside and forest.

Phoroncidia scutula (Nicolet)
Figures 19–22

Gasteracantha scutula Nicolet, 1849: 478, pl. 5, fig. 6, ♀. Female holotype from Chile, in the Muséum National d'Histoire Naturelle, Paris.

Phoroncidia scutula, —Levi, 1964b: 73, figs. 18–20, ♂.

Description. Female. Brown, usually with white pigment on dorsum of abdomen and sometimes with black areas. The color does not change in alcohol. The abdomen has three humps; the anterior ones are more distinct in immature females. The carapace is highest behind the eyes and has a pronounced ridge. The shape of the abdomen distinguishes *P. scutula* from *P. margamarga*. Total length, 2.5 mm. Carapace, 0.95 mm long, 1.0 mm wide. First patella and tibia, 0.60 mm; second, 0.52 mm; third, 0.40 mm. Fourth femur, 0.80

mm; patella and tibia, 0.80 mm; metatarsus, 0.40 mm; tarsus, 0.34 mm.

Habits. All specimens were collected by sweeping in forested or shaded areas. More males than females were collected, perhaps because females sit on bark or on stems. Previously only males were available for examination. Males and females are mature in February and March.

Phoroncidia margamarga Levi
Figures 16–18

Phoroncidia margamarga Levi, 1964b: 77, figs. 30–34, ♀. Female holotype from Marga Marga, Valparaíso Prov., in the Institut Royal des Sciences Naturelles de Belgique, Brussels.

Description. Male. Carapace and sternum brown. Legs banded. Abdomen dark brown with white pigment areas, larger on dorsum than venter. The abdomen is slightly wider than long and has a median dorsal tubercle. Total length, 1.5 mm. Carapace, 0.6 mm wide, 0.6 mm long. First femur, 0.60 mm; patella and tibia, 0.59 mm; metatarsus, 0.30 mm; tarsus, 0.28 mm. Second patella and tibia, 0.48 mm; third, 0.40 mm; fourth, 0.58 mm.

Heretofore the male had been unknown. The shape of the abdomen (Figs. 17, 18) is probably more distinct than the palpus (Fig. 16).

Additional record. Osorno: Termas de Puyehue, 240 m, 14 March 1965, ♂.

Phoroncidia puyehue sp. n.
Figures 23–26

Holotype. Female from Termas de Puyehue, Osorno, Chile, 10 March 1965, 250 m, collected in forest by sweeping vegetation (H. Levi), in the Museum of Comparative Zoology. The species is named after the type locality; the specific name is a noun in apposition.

Description. Carapace and sternum dark brown. Legs light, with distal segments banded. Abdomen white with pigment spots and black patches. Spinnerets ringed with black, and area between epigastric groove and spinnerets white; epigynum black. Total length, 2.10 mm. Carapace, 0.73 mm long, 0.70 mm wide. First patella and tibia, 0.60 mm; second, 0.52 mm; third, 0.42 mm. Fourth femur, 0.59 mm; patella and tibia, 0.65 mm; metatarsus, 0.30 mm; tarsus, 0.29 mm.

Diagnosis. This species of *Phoroncidia* differs from others by having three pairs of lateral and one dorsal median hump on the abdomen (Figs. 25, 26), besides many tiny sclerotized spots. The genitalia are illustrated by Figures 23 and 24. The epigynum, like that of other members of the genus, is an indistinct structure.

Argyrodes ?elevatus Taczanowski

Argyrodes elevatus Taczanowski, 1873: 120, pl. 5, fig. 12, ♀. Female holotype from "Uassa French Guiana" [Rio Uaça, Amapa, Brazil], in the Polish Academy of Sciences. Exline and Levi, 1962: 134, figs. 128–132, ♀♂, map 5.

The only specimens collected were juveniles and a mature female whose genitalia are covered by exudate. Thus the determination is uncertain. The specimens were collected in the web of *Metepeira* and are in the American Museum of Natural History.

Record. Coquimbo: Salamanca, Fundo Tahuinco, 1 May 1961 (A. F. Archer).

Enoplognatha zapfeae Levi, emend.

Enoplognatha zapfei Levi, 1962a: 19, figs. 14, 15, ♀. Female holotype from Putre, Prov. Tarapacá, in the Museum of Comparative Zoology. The species was named for Señora H. Zapfe de Mann.

Steatoda ancorata (Holmberg)

Theridium ancoratum Holmberg, 1874: 72, fig. 16. Holotype lost.

Steatoda ancorata, —Levi, 1962a: 34, figs. 40–47, ♀♂.

This widespread species occurs in arid areas, under stones, or among rocks. It has been collected in Tumbre, Antofagasta and Natales, Magallanes, Chile.

Additional record. Llanquihue: Petrohué, on buildings, 20–21 March 1965; it is

probably also found among the cinders of Volcan Osorno around Petrohué.

"Theridion" funerarium Nicolet

Theridion funerarium Nicolet, 1849: 537. The juvenile syntypes have two dorsal longitudinal stripes on the abdomen. The sternum is black. From Chile, the specimens are in the Muséum National d'Histoire Naturelle, Paris; examined. The coloration resembles that of *Coleosoma floridanum* Banks but this cosmopolitan species has not so far been found in Chile.

MIMETIDAE

Ero spinipes (Nicolet), new combination
Figures 48–53

Theridion spinipes Nicolet, 1849: 540. Juvenile female lectotype from Chile here designated, in the Muséum National d'Histoire Naturelle, Paris; examined.

?Ero nicoleti Simon, 1904: 96. Holotype from La Herradura, Coquimbo, in the Muséum National d'Histoire Naturelle, Paris; not examined.

Note: The juvenile specimen designated as lectotype (Fig. 48) is 2.5 mm long, and is in poor physical condition. The first legs have macrosetae as do other mimetids. Specimens collected by A. F. Archer, determined by him as *Ero nicoleti* Simon, and deposited in the American Museum in New York, appear to be conspecific. The illustrations were made from the Archer specimens.

Records. Valparaíso: Bosque de Quintero, May 1961. *Malleco*: Bosque de Collipulli, Dec. 1961. *Llanquihue*: Puerto Montt, Isl. Tenglo, March 1962; 2–3 km NW of Ensenada, 18 March 1965, ♀ (H. Levi).

LINYPHIIDAE

"Ceratinopsis" modesta (Nicolet)
Figures 45–47

Theridion modestum Nicolet, 1849: 526. Female lectotype here designated, from Chile, is in the Muséum National d'Histoire Naturelle, Paris.

Erigone modesta, —Keyserling, 1886: 229, pl. 19, fig. 284, ♀.

Ceratinopsis modesta, —Simon, 1894: 644–645.

Note: Keyserling correctly identified this linyphiid spider, described the species, and also synonymized with it *Theridium weyenberghii* Holmberg, 1874, page 79. According to Keyserling, this species, which has a bright red abdomen when alive, is also found in Argentina and Rio Grande du Sul, Brazil.

Records. Two ♀ paralectotypes were with the lectotype.

"Ceratinopsis" distincta Nicolet
Figures 43–44

Theridion distincta Nicolet, 1849: 526. Female lectotype here designated, from Chile, is in the Muséum National d'Histoire Naturelle, Paris; examined.

Ceratinopsis distincta, —Petrunkevitch, 1911: 224.

Description. The best preserved specimen has a light brown cephalothorax, with the legs lightest, and an indistinct longitudinal row of spots on the dorsum of the abdomen. The diameter of the anterior median eyes is half that of the others. The anterior median eyes are two diameters apart, three diameters from laterals. The posterior median eyes are one diameter apart, one and one-half from laterals. Like *"C." modesta*, the legs have few strong spines. Total length, 3.2 mm. Carapace, 1.2 mm long, 1.0 mm wide. First patella and tibia, 1.2 mm; second, 1.0 mm; third, 1.0 mm. Fourth femur, 1.3 mm; patella and tibia, 1.4 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Records. Two paralectotypes were originally in the vial with the lectotype.

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Bulletin OF THE
Museum of
Comparative
Zoology

Habitat Observations, Records, and New South American Theridiid Spiders (Araneae, Theridiidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 2
SEPTEMBER 29, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
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Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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HABITAT OBSERVATIONS, RECORDS, AND NEW SOUTH AMERICAN THERIDIID SPIDERS (ARANEAE, THERIDIIDAE)

HERBERT W. LEVI

In a recent paper, Bonnet (1966) tells us that two-thirds of the spiders described have never been found again, and that of more than 22,000 spider species known in 1939, less than 3,000 are common or well described. This sorry record is evidence of the inadequacy of descriptions made by arachnologists who are often more interested in giving names than in studying the animals at hand. Bonnet cites as causes poor descriptions and insufficient bibliographic searches, but to these should be added the historic reluctance of many museum curators to let the biologists look at holotypes, as they must in order to make the needed revisions. Although this is mainly a problem of the past, yet even today several museums, following obsolete rules, so protect type specimens that their study can be arranged only years after the revision is completed. And when such study must be undertaken during a costly but hurried visit to the museum, often one finds the museum insufficiently equipped for the examination of small animals. Taking one's own equipment along complicates the customs passage and is made expensive by weight limits of airlines. However, I am grateful for the cooperation of the various curators who have made their collections and holotypes available to me. It is encouraging to find that a large proportion of the theridiid species described from South America have been rediscovered in the collections that have accumulated over the years in various museums.

These additional notes on the Theridiidae resulted from my visit to South America in 1965. I was able to see and work with the living spiders, and when possible made photographs and took notes on the habitats and habits. Also, I was able to examine the important Mello-Leitão collection in Rio de Janeiro. An earlier paper considered the spiders of Chile, which has its own, almost entirely endemic, fauna. This paper also contains additions and corrections to my previous papers on South American theridiid spiders. Another reason that drew me to South America, the field study of black widows, *Latrodectus*, is outside the scope of this paper.

I am very grateful to numerous colleagues who helped me. In Peru, Dr. H.-W. Koepcke and Dr. Maria Koepcke directed me to collecting places. Dr. P. Aquilar F. of San Marcos University took me into the field with his car every day I was in Lima. Dr. F. Carrasco Z. of Cuzco University took me to Urubamba and helped me collect. Dr. J. Abalos accompanied me and helped me in the field in northern Argentina. Prof. Dr. M. Birabén, Prof. R. D. Schiapelli, Mrs. B. Gerschman de Pikelin, Prof. M. E. Galiano and Dr. A. Barrio extended their hospitality to me in Buenos Aires. Dr. P. Vanzolini and Mr. P. de Biasi helped me reach the field in the São Paulo area. Dr. J. L. de A. Feio, Miss A. Timotheo da Costa, and Dr. J. de M. Carvalho and Director Dr. N. Santo permitted me to examine the valuable Mello-Leitão collection. Mr. Johann

Becker spent a great amount of his valuable time accompanying me in the surroundings of Rio and in the Organ Mountains and Teresópolis.

The paper is divided into two parts: first, corrections to previous papers, and second, notes, observations, and descriptions of new theridiid spiders.

ADDITIONS AND CORRECTIONS TO PREVIOUS PAPERS

After publication of my paper on South American arachnologists (Levi, 1964), a valuable letter was received from Dr. A. Riedel of the Polish Academy of Sciences. His comments, making corrections in the dates of the important Polish collector Jelski, were based on the archives of his institution. "Jelski left Poland in 1863 and stayed at first in the Balkans and France, but he visited Cayenne already in 1864. He left for Peru in 1870 and since 1874 worked in the Lima Museum and later returned to Poland in 1880."

Dr. H.-W. Koepcke and Dr. M. Koepcke made me aware that the locations of many of the old Peruvian collecting sites and haciendas can be found in German Stieglich's *Diccionario Geografico del Peru*, Lima, 1922. Few copies are to be found outside Peru, but there is one in the Harvard Widener Library. The area in which Jelski and Stolzman collected birds and spiders, the province of Tarma, Junín, was apparently chosen because of its great diversity in altitude, flora and fauna, reaching from the high Andes down to the haciendas of the Amazon Basin. It is a very fruitful area for collecting.

Corrections of Names

Euryopis notabilis (Keyserling, 1891) [Not *E. notabila*] Levi, 1963a:136.

Dipoena rubella (Keyserling, 1884) [Not *D. rubellum*] Levi, 1963a:167.

Achaearanea dromedariformis (Roewer, 1884) [Not *A. dromedariforma*] Levi, 1963b:205.

A. rioensis Levi, 1963b:209. Holotype from Teresópolis, Est. Rio de Janeiro [not Guanabara], Brazil. The species is named after the state of the type locality.

A. alacris (Keyserling, 1884) [Not *A. alacre*], Levi, 1963b:227.

A. pinguis (Keyserling, 1886) [Not *A. pingue*], Levi, 1963b:228.

NOTES, OBSERVATIONS, AND DESCRIPTIONS OF NEW SOUTH AMERICAN THERIDIID SPECIES

Achaearanea tepidariorum (C. L. Koch)

Theridium tepidariorum C. L. Koch, 1841, Die Arachniden, 8:75, figs. 646–648, ♀ ♂. Syntypes from greenhouses at the University of Erlangen, Bavaria.

Achaearanea tepidariorum,-Levi, 1955, Amer. Mus. Novit., No. 1718:32, figs. 69, 70, 83, 84, ♀ ♂; 1963, Bull. Mus. Comp. Zool., 129:215, map.

Collections. Specimens were collected on buildings in Tucumán, Argentina, and on top of Corcovado Mountain, Rio de Janeiro, in Teresópolis, but also (probably on buildings) at 1,850 m in the Serra dos Orgãos, Est. Rio de Janeiro, Brazil.

Achaearanea hieroglyphica (Mello-Leitão), new combination

Achaea hieroglyphica Mello-Leitão, 1940, Arq. Zool, São Paulo, 2:202. Female holotype from from Colatina, Espírito Santo, Brazil, in the Museum Nacional, Rio de Janeiro; examined.

Chrysso pentagona Caporiacco, 1954, Comm. Pontifica Acad. Sci., 16:75, fig. 12, ♀. Female holotype from Goudronville, French Guiana, in the Muséum National d'Histoire Naturelle, Paris; examined. NEW SYNONYMY.

Achaearanea pentagona,-Levi, 1963, Bull. Mus. Comp. Zool., 129:202, figs. 1–3, ♀.

This species has also been collected in Huánuco State of Peru.

Achaearanea rioensis Levi

Achaearanea rioensis Levi, 1963, Bull. Mus. Comp. Zool., 129:209, figs. 36–38. Male holotype from Teresópolis, 900–1,000 m, Est. Rio de Janeiro, Brazil, in the American Museum of Natural History.

Collections. On top of Pico Corcovado, 700 m, Rio de Janeiro, Brazil.

Achaearanea hirta (Taczanowski)

Argyrodes hirtus Taczanowski, 1873, Horae Soc. Ent. Rossicae 9:119. Female syntypes from

Cayenne, French Guiana, in the Polish Academy of Sciences, Warsaw; examined.

Achaearanea hirta,-Levi, 1959, Bull. Mus. Comp. Zool., 121:70, figs. 35–38, ♀ ♂, map. Levi, 1963, *ibid.*, 129:212, map.

Collections. Specimens were collected in Tucumán, Argentina, on the outside of buildings of the Instituto Miguel Lillo. This is the southernmost record of the species.

Achaearanea passiva (Keyserling)

Theridium passivum Keyserling, 1891, Die Spinnen Amerikas, 3:195, pl. 7, fig. 141, ♀. Female holotype from Faz. Calvario, Est. Rio de Janeiro, Brazil, in the British Museum; examined.

Achaearanea passiva,-Levi, 1963, Bull. Mus. Comp. Zool., 129:207, figs. 26–28, ♀ ♂.

Collections. This southeastern Brazilian species was collected in the botanical garden, in forest, São Paulo, 10 April 1965 (P. de Biasi, H. Levi).

Achaearanea orgea sp. n.
Figures 5, 6

Holotype. Female from under stone in forest, Serra dos Orgãos, between 1,000 and 1,500 m, 20 April 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Prosoma and legs dark orange-brown. Abdomen with black patches and a white line descending on each side, almost meeting on dorsum; there is a median dorsal white spot and a spot behind each white line on dorsum. Anterior median eyes slightly smaller than others, their diameter apart, less than a diameter from laterals. Posterior median eyes more than a diameter apart, less than their diameter from laterals. Abdomen almost spherical. Total length, 3.1 mm. Carapace 1.4 mm long, 1.4 mm wide. First femur, 1.8 mm; patella and tibia, 2.0 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 1.4 mm; third, 1.0 mm; fourth, 1.7 mm.

Diagnosis. This species might be either a *Theridion* or *Achaearanea*. It differs from *Theridion macuchi* Levi from Ecuador by being larger, and the epigynum (Fig. 6) does not have a knob. It differs in coloration and larger size from *Achaearanea analista* Levi, from southeastern Brazil.

Echinotheridion cartum Levi

Echinotheridion cartum Levi, 1963, Bull. Mus. Comp. Zool., 129:236, figs. 117–121, ♀. Female holotype from Apa River, Paraguay, in the American Museum of Natural History.

Collections. BRAZIL. *Guanabara*: in forest, Pico da Tijuca, 500–950 m, 17 April 1965; in park, Jardim Botânico, Rio de Janeiro, 18 April 1965.

Theridion calcynatum Holmberg
Figure 1

Theridion calcynatum Holmberg, 1876, An. Agric. Rep. Argentina, 4:72. Types from Argentina lost.—Levi, 1963, Bull. Mus. Comp. Zool., 129:548, figs. 100–107, ♀ ♂, map 3.

Distribution. South America (except Chile) from Venezuela to Argentina.

Collections. PERU. *Lima*: Lima, in garden on the undersides of leaves and shrubs. *Cuzco*: Urubamba River near Machu-Picchu, collected by sweeping in rain forest; Urubamba, Feb. 1965 (F. Carrasco). BRAZIL. *Est. Rio de Janeiro*: forest, Serra dos Orgãos, 1,000–1,800 m. *Guanabara*: forest, Pico da Tijuca, 500–900 m. *São Paulo*: forest, in botanical garden, São Paulo.

Theridion rufipes Lucas

Theridion rufipes Lucas, 1846, Explor. Scient. de l'Algérie. Zool., 2(1):263, pl. 16, fig. 5, ♀. Female holotype from near Oran, Algiers.—Levi, 1957, Bull. Amer. Mus. Nat. Hist., 112: 56, figs. 188–193, ♀ ♂.

Distribution. Pantropical, in or on buildings.

Collections. PERU. *Lima*: females collected in the corner of the kitchen of a house in Miraflores, tightly appressed against the wall, with only a small web. The habitat in Peru was like that of Florida specimens I have collected. BRAZIL.

Figure 1. *Theridion calcynatum* Holmberg in web, garden in Lima, Peru.
Figure 2. *Anelosimus studiosus* (Hentz), dense web in shrub, Barra da Tijuca, Rio de Janeiro, Brazil.

Guanabara: on buildings on Corcovado, 700 m. *Est. Rio de Janeiro*: in corner inside house in Teresópolis.

Theridion adamsoni Berland

Theridion adamsoni Berland, 1934, Bull. B. P. Bishop Mus., 113:102, figs. 6–9, ♀. Female syntypes from Tahiti in the Bishop Museum, Honolulu; examined.

Theridion hobbsi,-Levi, 1957, Bull. Amer. Mus. Nat. Hist., 112:62, figs. 198–199, 209, 213–214, ♀♂, map 28.

Distribution. Pantropical.

Collections. ARGENTINA. *Tucumán*: outside on walls of building of Instituto Miguel Lillo in Tucumán, April 1965. This is the southernmost record in the Americas.

Theridion volubile Keyserling

Theridion volubile Keyserling, 1884, Die Spinnen Amerikas, 2(1):37, pl. 2, fig. 19, ♀. Female lectotype from Amable María, 640 m, Junín, Peru, in the Polish Academy of Sciences, Warsaw; examined.

Distribution. Venezuela to Arequipa, Peru.

Collections. PERU. *Junín*: San Ramón, 80 m, plantation on edge of rain forest, near the type locality.

Theridion evexum Keyserling

Theridion evexum Keyserling, 1884, Die Spinnen Amerikas, 2(1):65, pl. 3, fig. 39, ♀. Female holotype from Spanish colony N. Granada, in the British Museum; examined. —Levi, 1959, Bull. Mus. Comp. Zool., 121:97, figs. 124–135, ♀♂, map 5.

Distribution. From southern Mexico, West Indies, to southern Brazil.

Collections. BRAZIL. *Est. Rio de Janeiro*: under leaf in forest of Serra dos Orgãos, 1,000–1,500 m, 20 April 1965, ♀ (J. Becker, H. Levi).

Theridion triguttatum Keyserling

Theridion triguttatum Keyserling, 1891, Die Spinnen Amerikas, 3:190, pl. 6, fig. 136, ♀. Female syntypes from Nova Friburgo, Est. Rio de Janeiro and Espírito Santo on the Rio Minas, Brazil, in the British Museum; examined.—Levi, 1963, Bull. Mus. Comp. Zool., 129:542, figs. 76–77, ♀.

Distribution. Southeastern Brazil.

Collections. BRAZIL. *Guanabara*: Pico da Tijuca, 500–950 m, 17 April 1965, ♀ (J. Becker, H. Levi).

Theridion sexmaculatum Keyserling

Theridion sexmaculatum Keyserling, 1884, Die Spinnen Amerikas, 2(1):82, pl. 4, fig. 51, ♀. Female syntypes from Amazonas, Brazil, in the Hope Department of Entomology, Oxford University; examined.—Levi, 1959, Bull. Mus. Comp. Zool., 121:119, figs. 236–239, ♀♂.

Distribution. West Indies to Ecuador.

Collections. BRAZIL. *Guanabara*: Barra da Tijuca, sand dunes and dune vegetation, 16 April 1965, ♀ (J. Becker, H. Levi). This is the southernmost record.

Theridion plaumanni Levi

Theridion plaumanni Levi, 1963, Bull. Mus. Comp. Zool., 129:583, figs. 244–248, ♀♂, map 3. Female holotype from Nova Teutônia, Santa Catarina, Brazil, in the Senckenberg Museum, Frankfurt.

The species, otherwise colorless, has a tiny black spot on the anterior face of each patella and distal end of each tibia.

Distribution. From Venezuela to southern Brazil.

Collections. BRAZIL. *São Paulo*: Camino del mar, 33 km south of São Paulo, in vegetation, 11 April 1965, ♀ (P. de Biasi, H. Levi).

Theridion humboldti sp. n.
Figures 7–9

Holotype. Female from Miraflores, under leaf in garden, Lima, Peru, 6 Feb. 1965 (H. Levi), in the Museum of Comparative Zoology. This species is named after the explorer, A. von Humboldt.

Description. Carapace, sternum, legs light yellow-brown. Abdomen with white pigment spots on dorsum, three pairs of black patches, the last one running to spinnerets and fusing (Fig. 7). Area between, close to spinnerets, white. Venter with a black spot on each side of spinnerets. On each side of abdomen, a black streak. Eyes subequal in size, anterior median eyes one

diameter apart, their radius from laterals. Posterior eyes a little more than a diameter from each other. Total length, 5 mm. Carapace 2.0 mm long, 1.7 mm wide. First femur, 3.0 mm; patella and tibia, 3.0 mm; metatarsus, 2.7 mm; tarsus, 0.8 mm. Second patella and tibia, 2.1 mm; third, 1.5 mm; fourth, 2.5 mm.

Diagnosis. Theridion humboldti differs from *T. calcynatum* by having two black spots on a common depression in the epigynum (Fig. 9), and heavily sclerotized wide connecting ducts (Fig. 8).

Chrysso pulcherrima (Mello-Leitão), new combination

Argyrodes pulcherrimus Mello-Leitão, 1917, Broteria, 15:86, figs. 7, 8, ♀. Female holotype [fragments] from Manguinhos, Dist. Fed. [Est. Guanabara], Brazil, in the Museu Nacional, Rio de Janeiro; examined.

Meotipa clementinae Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30:212, fig. 61, ♀. Female holotype from Puerto Rico, at the Peabody Museum, Yale University, New Haven. NEW SYNONYMY.

Chrysso clementinae,-Levi, 1962, Psyche, 69:231, figs. 71–75, ♀ ♂, map 1.

Note. Argyrodes pulcherrimus Mello-Leitão is not a synonym of *A. elevatus* (Taczanowski) as thought by Exline and Levi, 1962, Bull. Mus. Comp. Zool., 127(2): 135.

Thymoites palo sp. n.
Figures 10–12

Holotype. Female from Camino del mar, forest and fields 33 km south of São Paulo, Brazil, 11 April 1965 (P. de Biasi, H. Levi), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace yellow, eye area black. Sternum yellowish. Legs yellow except fourth, which has distal end of femur and distal end of tibia black (Fig. 10). Abdomen yellowish white except for two black spots, one behind the other, posterior one just above spinnerets. Anterior median eyes smallest, one and one-half diameters from each other, one and one-half diameters from laterals. Posterior median eyes one and one-half diameters apart, two diameters from laterals. Total length, 1.3 mm. Carapace 0.69 mm long, 0.60 mm wide. First femur, 0.70 mm; patella and tibia, 0.69 mm; metatarsus, 0.42 mm; tarsus, 0.36 mm. Second patella and tibia, 0.54 mm; third, 0.43 mm; fourth, 0.65 mm.

Diagnosis. Thymoites palo differs from *T. villaricaensis* Levi from Paraguay in having smaller eyes, and by its coloration (Fig. 10).

Thymoites urubamba sp. n.
Figures 13, 14

Holotype. Female from Urubamba River forest below Machu-Picchu ruins, on vegetation, 2,000 m, Cuzco, Peru, 21 Feb. 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, orange. Legs orange-brown, coxae and patellae much lighter. Abdomen yellow-white, without markings. Eyes silvery, without any black, and relatively small, subequal in size. Laterals on a joint small tubercle. Anterior median eyes two diameters apart, less than one diameter from laterals. Posterior eyes one and one-half diameters apart. Height of clypeus about four diameters of anterior median eyes. Abdomen oval, pointed behind. Total length, 1.8 mm. Carapace 0.8 mm long, 0.7 mm wide. First femur, 0.9 mm; patella and tibia, 0.9 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 0.8 mm; third, 0.6 mm; fourth, 0.8 mm.

Diagnosis. The ducts of this species are black (Figs. 13, 14), and quite similar to those of *Thymoites ebus* Levi from Brazil. However, the coils in *T. urubamba* are posterior to the seminal receptacles (Fig. 13), while in *T. ebus* they loop anteriorly.

Thymoites machu sp. n.
Figures 15, 16

Holotype. Female from Urubamba River forest below Machu-Picchu ruins, 2,000 m

Distribution of *Tidarren fordum*. Numerous literature records of the species from Argentina were not mapped.

elevation, on vegetation, Cuzco, Peru, 21 Feb. 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum orange. Legs orange-brown; patella and coxae lighter; distal segments darker. Abdomen orange-white, without markings. Eyes silver with black rings. Anterior median eyes largest, their diameter apart, one-third their diameter from laterals. Posterior median eyes two diameters apart, one and one-half diameter from laterals. Total length, 1.6 mm. Carapace 0.6 mm long, 0.6 mm wide. First femur, 1.2 mm; patella and tibia, 1.8 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 0.7 mm; third, 0.6 mm; fourth, 0.9 mm.

Diagnosis. *Thymoites machu* is similar to *T. ilvan* Levi from Brazil but the ducts are straight and not undulating (Fig. 15).

TIDARREN Chamberlin and Ivie, 1934

No additional new species from South America have been found that belong to this genus. The minute males almost never are collected, although as many as ten have been seen in the web of a young female in Florida. Unlike members of *Achaearanea*, the female *Tidarren* nests in a rolled-up dead leaf in the middle of the web.

Misplaced species, described as *Tidarren*, from South America and Central America include:

Tidarren incertissimum Caporiacco = *Theridion incertissimum* (Caporiacco).

Tidarren fordum (Keyserling)

Map

Theridion fordum Keyserling, 1884, Die Spinnen Amerikas, 2(2):387, pl. 1, fig. 9, ♀. Female holotype from "Sta. Fé de Bogotá" [Bogotá, Colombia], in the British Museum; examined.

?*Theridion maculosum* Keyserling, 1884, *Op. cit.* 2 (2):30, pl. 1, fig. 14, ♀. Female holotype from Venezuela ["Caracas" on specimen], in the Institut Royal des Sciences Naturelles de Belgique, Brussels; examined.

Tidarren fordum,-Levi, 1955, J. New York Entomol. Soc., 63:73, figs. 49–57, 61–64, map.

Bertkau's description of *Theridium haemorrhoidale* (1880, Mém. Cour. Acad. Belgique, 43:78; holotype from Rio de Janeiro, lost) fits Brazilian specimens of this species. However, the type could not be located in Brussels, Bonn, or Frankfurt. The type of *T. maculosum* Keyserling is shrivelled up and in a poor state of preservation. It is smaller, but within the range of variation, and the abdomen is not higher than long (probably because it is shrivelled). While it is probable that specimens assigned to this species from North America to Colombia are all one species, it is possible (but unlikely) that several South American species are confused, as there are hardly any of the minute males of *Tidarren* in collections.

Distribution. Southern United States to Chile and Argentina (map). As the Argentine records are from the literature only, they have not been mapped.

COLEOSOMA O. P.-Cambridge 1882

The genus *Coleosoma* is unique in a number of ways. Three species having a wide distribution are known from the Americas. During my study of American theridiid spiders, no additional species were found. The numerous new records are listed below, as no common characteristic of their niches could be found. The males of all three species appear to be ant mimics, an observation first made by Mr. J. Beatty in Florida (unpubl.), while the females are web spiders living under vegetation. Not only do the species live in undisturbed habitats, but live *Coleosoma floridanum* appear frequently in shipping boxes, arriving in the United States from other parts of the world.

Coleosoma acutiventer (Keyserling)

Achaea acutiventer Keyserling, 1884, Die Spinnen Amerikas, 2(1):113, fig. 74, ♀. Female holotype from Maragnioe [Maraynioc, Junín, Prov. Tarma], Peru, in the Polish Academy of Sciences, Warsaw; examined.

Coleosoma acutiventer,-Levi, 1959, Breviora, Mus. Comp. Zool., No. 110:4, figs 6–11, ♀♂, map 1.

The cymbium of the palpus of Peruvian specimens is more swollen than that of specimens from the northern portions of its range.

Distribution. Southeastern United States to southern Brazil.

Additional records. VENEZUELA. *Dist. Fed.*: Caracas, 1887–1888 (E. Simon). *Carabobo*: San Estebán, 1888 (E. Simon). COLOMBIA. *Amarca*: Guaduas (E. I. Schlinger, E. S. Ross). ECUADOR. *Napo-Pastaza*: Río Topo (H. E., D. L. Frizzell); *Guayas*: Guayaquil (H. E., D. L. Frizzell). *El Oro*: Buena Vista, 25 km SE of Machala (R. Walls). PERU. *Huánuco*: 100 km E of Tingo María, ♀ (E. I. Schlinger, E. S. Ross). BRAZIL. *Minas Gerais*: Caraça, 2

♀ [vial with 2 ♀ labelled "Caraça. Parag.," in Paris Museum]; *Est. Rio de Janeiro*: under logs and stones, Serra dos Orgãos, 1,500 m, 20 April 1965, ♀ (J. Becker, H. Levi).

Coleosoma floridanum Banks

Coleosoma floridana Banks, 1900, Canadian Entomol., 32:98. Male syntypes from Punta Gorda, Florida, in the Museum of Comparative Zoology; examined.

Coleosoma floridanum,-Levi, 1959, Breviora, Mus. Comp. Zool., No. 110:6, figs. 12–17, ♀ ♂, map 2.

Distribution. Pantropical, southeastern United States, Central America, West Indies to central Peru and Brazil.

Additional records. VENEZUELA. *Mérida*: Timotes (in Frankfurt Museum); *Dist. Fed.*: Caracas (E. Simon); La Guaira, 1887–1888 (E. Simon). *Carabobo*: San Estebán, 1888 (E. Simon). BRITISH GUIANA: Georgetown (A. M. Nadler). FRENCH GUIANA: Cayenne (A. M. Nadler). ECUADOR. *Guayas*: Milagro (H. E., D. L. Frizzell); Guayaquil (H. E., D. L. Frizzell). PERU. *Huánuco*: Monzón Vall., Tingo María (E. I. Schlinger, E. S. Ross). BRAZIL. *Pará*: in package which arrived from Belém in Cambridge, Mass., 7 Nov. 1961, ♀. *Pernambuco*: Recife (in Frankfurt Museum).

Coleosoma normale Bryant

Coleosoma normale Bryant, 1944, Psyche, 51:56, figs. 2, 5, 8, 10, ♀ ♂. Male holotype from Fort Myers, Florida, in the Museum of Comparative Zoology; examined.—Levi, 1959, Breviora, Mus. Comp. Zool., No. 110:3, figs. 1–5, ♀ ♂, map 1.

Distribution. North Carolina, Arizona, to southern Brazil (previously known only from northern South America).

Collection. BRAZIL. *Est. Rio de Janeiro*: among logs and stones, Serra dos Orgãos, 1,500 m, 20 April 1965, ♀ (J. Becker, H. Levi).

Helvibis chilensis (Keyserling) Figures 17–21

Formicinoides chilensis Keyserling, 1884, Die Spinnen Amerikas, 2(1):215, pl. 10, fig. 129, ♀. Female holotype "from Chile," in the Muséum National d'Histoire Naturelle, Paris; examined.

Helvibis chilensis,-Levi, 1964, Trans. Amer. Microscop. Soc., 83:135, figs. 1–6, ♀.

Description. Male. Carapace, sternum, dark brown. Legs, including coxae, light brown; abdomen with scutum dark brown, soft area gray to whitish. Cephalothorax as illustrated, striated with fine grooves; stalk finely annulated; sternum punctate. Anterior median eyes one and one-half diameters apart, one diameter from laterals. Posterior median eyes a little less than one diameter apart, one and three-quarters diameters from laterals; eyes subequal in size. Abdomen with the ventral shield (Fig. 19). Total length, 3.5 mm. Carapace, 2.2 mm long, 1.0 mm wide. First femur, 4.0 mm; other segments broken off. Second patella and tibia, 2.1 mm; third, 1.3 mm; fourth, 2.5 mm.

Discussion. This species was known only from the type, coming from "Chile." The type locality has been questioned. The male that probably belongs to this species comes from the Amazon Basin, as do all other species of *Helvibis*.

Record. BRAZIL. *Amazonas*: Benjamin Constant, Sept. 1963, ♂ (K. Henks, São Paulo Museum).

Episinus cognatus O. P.-Cambridge

Episinus cognatus O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1:109, pl. 15, fig. 2, ♂. Male holotype from Teapa, Tabasco, Mexico, in the British Museum.-Levi, 1955, J. New York Entomol. Soc., 62:71, figs. 8–10, 21, 22, 33, 41, ♀ ♂; 1964, Bull. Mus. Comp. Zool., 131:13, map.

The southernmost record of this species is Quincemil, 750 m, Cuzco, Peru, Sept. 1962 (L. Peña).

Episinus rio sp. n. Figures 22–24

Holotype. Female, from sweeping in forest on Pico da Tijuca, 500 to 950 m, Rio de Janeiro, Est. Guanabara, 17 April 1965 (H. Levi), in the Museum of Comparative Zool-

ogy. The specific name is an arbitrary combination of letters.

Description. Carapace yellow-brown with a black line around margin, eye area reddish. Sternum black. Distal ends of leg segments darker. Transverse black pigment band at widest part of abdomen. Anteriorly, two lateral dark patches; venter with black pigment, darker posteriorly. Two distinct horns between eyes. Anterior median eyes largest, others silvery with small lenses on modified opaque lens. Abdomen subtriangular without nipples, but with two distinct depressions on dorsum (Fig. 24). Total length, 1.9 mm. Carapace, 0.8 mm long, 0.8 mm wide. First femur, 1.6 mm; patella and tibia, 1.8 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second patella and tibia, 1.0 mm; third, 0.6 mm; fourth, 1.4 mm.

Diagnosis. This species is close to *Episinus bicruciatus* (Simon) but differs in that the median area of the epigynum is wider than long (Fig. 23), while in *E. bicruciatus* it is longer than wide. It differs from *E. aspus* Levi by lacking the anterior median dark area.

Episinus cuzco sp. n.
Figures 25–27

Holotype. Female and juvenile paratype from road up to Machu-Picchu ruins from railroad station, 2,100 m, in forest, Cuzco, Peru, 20 Feb. 1965 (H. Levi), in the Museum of Comparative Zoology. The species is named after the type locality, the specific name being a noun in apposition.

Description. Carapace whitish with a wide dark band on each side. Sternum and legs whitish. The anterior two-thirds of abdomen has scattered white and black pigment and some black pigment near posterior tip. Venter without pigment. Eyes silvery, except anterior medians, and with very small lenses on tubercle which is a modified lens. Abdomen with median dorsal tubercle (Fig. 25). Total length, 2.0 mm. Carapace 0.8 mm long, 0.8 mm wide. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 1.9 mm; tarsus, 0.6 mm. Second patella and tibia, 1.1 mm; third, 0.8 mm; fourth, 1.3 mm.

Diagnosis. This species keys out to *Episinus juarezi* Levi but differs in the structure of the seminal receptacles and the epigynum (Figs. 26, 27).

Thwaitesia affinis O. P.-Cambridge
Figure 3

Thwaitesia affinis O. P.-Cambridge, 1882, Proc. Zool. Soc. London:431, pl. 31, fig. 8a, ♀♂. Syntypes from the "Amazon," in the Hope Department of Entomology, Oxford; examined. —Levi, 1963, Psyche, 70:231, figs. 14–19, ♀♂, map 2.

This species has been collected from under leaves in open shrubby vegetation, both near the city of São Paulo, and Barra da Tijuca, Est. Guanabara, Brazil.

Anelosimus ethicus (Keyserling)

Theridium ethicum Keyserling, 1884, Die Spinnen Amerikas, 2(1):44, pl. 2, fig. 24, ♂. Male holotype from Rio de Janeiro, Brazil, in the Naturhistorisches Museum, Vienna; examined.

Anelosimus ethicus,-Levi, 1956, Trans. Amer. Microscop. Soc., 75:416, figs. 25, 28–30 ♀♂; 1963, *Ibid.*, 82:34.

The living spider has reddish pigment on dorsum of abdomen, particularly on sides of longitudinal band.

Distribution. Brazil from Ceara to Rio Grande do Sul.

Collections. BRAZIL. *São Paulo*: forest of botanical garden, in shrub, web in curled up leaves, ♀♂ (P. de Biasi, H. Levi).

Anelosimus studiosus (Hentz)
Figure 2

Theridion studiosum Hentz, 1850, J. Boston Soc. Natur. Hist., 6:274, pl. 9, fig. 5; holotype lost.

Anelosimus studiosus,-Levi, 1956, Trans. Amer. Microscop. Soc., 75:418, figs. 21–23, 37–39, map; 1963, *Ibid.*, 82:36.

Distribution. From eastern United States, eastern Mexico, Peru, to Argentina.

Collections. BRAZIL. *São Paulo*: forest of botanical garden, in shrubs in curled up leaves, ♀. *Est. Guanabara*: dense web in shrubs, Barra da Tijuca, ♀.

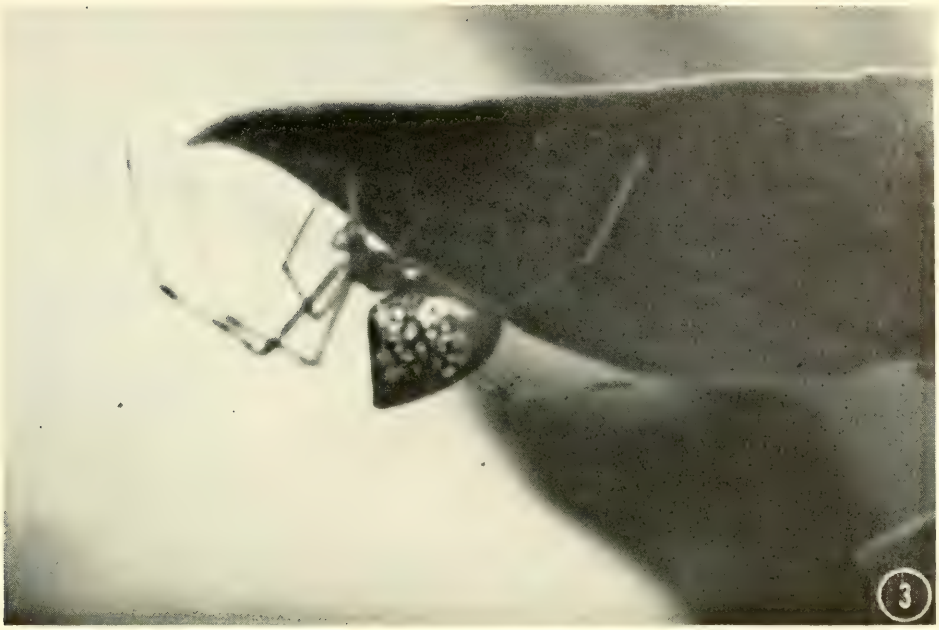


Figure 3. *Thwaitesia affinis* O. P.-Cambridge. Female under leaves near São Paulo, Brazil.

Figure 4. *Argyrodes longissimus* (Keyserling). Collected sweeping along forest, Urubamba River near Machu-Picchu, Cuzco, Peru; picture taken several minutes after being placed on a plant.

Wirada tijuca sp. n.
Figures 28–31

Holotype. Male from Pico da Tijuca, 500–950 m, in forest, Rio de Janeiro, Est. Guanabara, Brazil, 17 April 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the type locality.

Description. The whole animal is brown to black, depending on the amount of sclerotization. Carapace and sternum with tubercles. Anterior median eyes largest, almost touching, less than their radius from laterals. Posterior median eyes more than two diameters apart, one diameter from laterals. Dorsum of abdomen is a circular, convex, heavily sclerotized, highly polished disc (Fig. 28). Venter with sclerotized plates as in Figure 29, the dorsal plate overhanging all around. Total length, 1.5 mm. Carapace 0.57 mm long, 0.65 mm wide. First femur, 0.54 mm; patella and tibia, 0.50 mm; metatarsus, 0.30 mm; tarsus, 0.30 mm. Second patella and tibia, 0.44 mm; third, 0.40 mm; fourth, 0.50 mm.

Diagnosis. This species is separated from the other two species of *Wirada*, known from Venezuela to Ecuador, by the structure of the palpus (Figs. 30, 31).

Argyrodes longissimus (Keyserling)
Figure 4

Ariamnes longissimus Keyserling, 1891, Die Spinnen Amerikas, 3:202, pl. 7, fig. 145. Syntypes from Est. Rio de Janeiro, Brazil, in the British Museum; examined.

Argyrodes longissimus,-Exline and Levi, 1962, Bull. Mus. Comp. Zool., 127:127, figs. 100–109, ♀ ♂, map 4.

Collection. PERU. *Cuzco*: An adult male was collected by sweeping in the rain forest along the Urubamba River near Machu-Picchu ruins at 2,000 m, 21 Feb. 1965. The species had previously been known only from southeastern Brazil. It was green in color when alive (Fig. 4).

Argyrodes brasiliensis (Mello-Leitão), new combination

Rhomphaea brasiliensis Mello-Leitão, 1919 (1920), Rev. Soc. Brasileira Sci., 3:174. Mature holotype from Pinheiro, Est. Rio de Janeiro, Brazil, in the Museu Nacional, Rio de Janeiro; examined.

Argyrodes honestus Exline and Levi, 1962, Bull. Mus. Comp. Zool., 127:110, figs. 14–15, 41–43, ♀ ♂, map 2. Male holotype from Nova Teutônia, Santa Catarina, in the Senckenberg Museum, Frankfurt. NEW SYNONYMY.

Distribution. Venezuela to southern Brazil.

Argyrodes projiciens (O. P.-Cambridge)

Rhomphaea projiciens O. P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, 1: 186, pl. 23, figs. 9, 10. Male, female syntypes from Teapa, Tabasco, Mexico, in the British Museum; examined.

Ariamnes feioi Mello-Leitão, 1947, Bol. Mus. Nac., Rio de Janeiro, N. S., Zool., 80:10, fig. 46. Female holotype from Rio Clara, Minas Gerais, Brazil, in the Museu Nacional, Rio de Janeiro; examined. NEW SYNONYMY.

Argyrodes projiciens,-Exline and Levi, 1962, Bull. Mus. Comp. Zool., 127:106, figs. 8–10, 29–31, ♀ ♂, map 2.

Distribution. Southern United States to Paraguay.

Argyrodes altissimus (Mello-Leitão), new combination
Figures 35–37

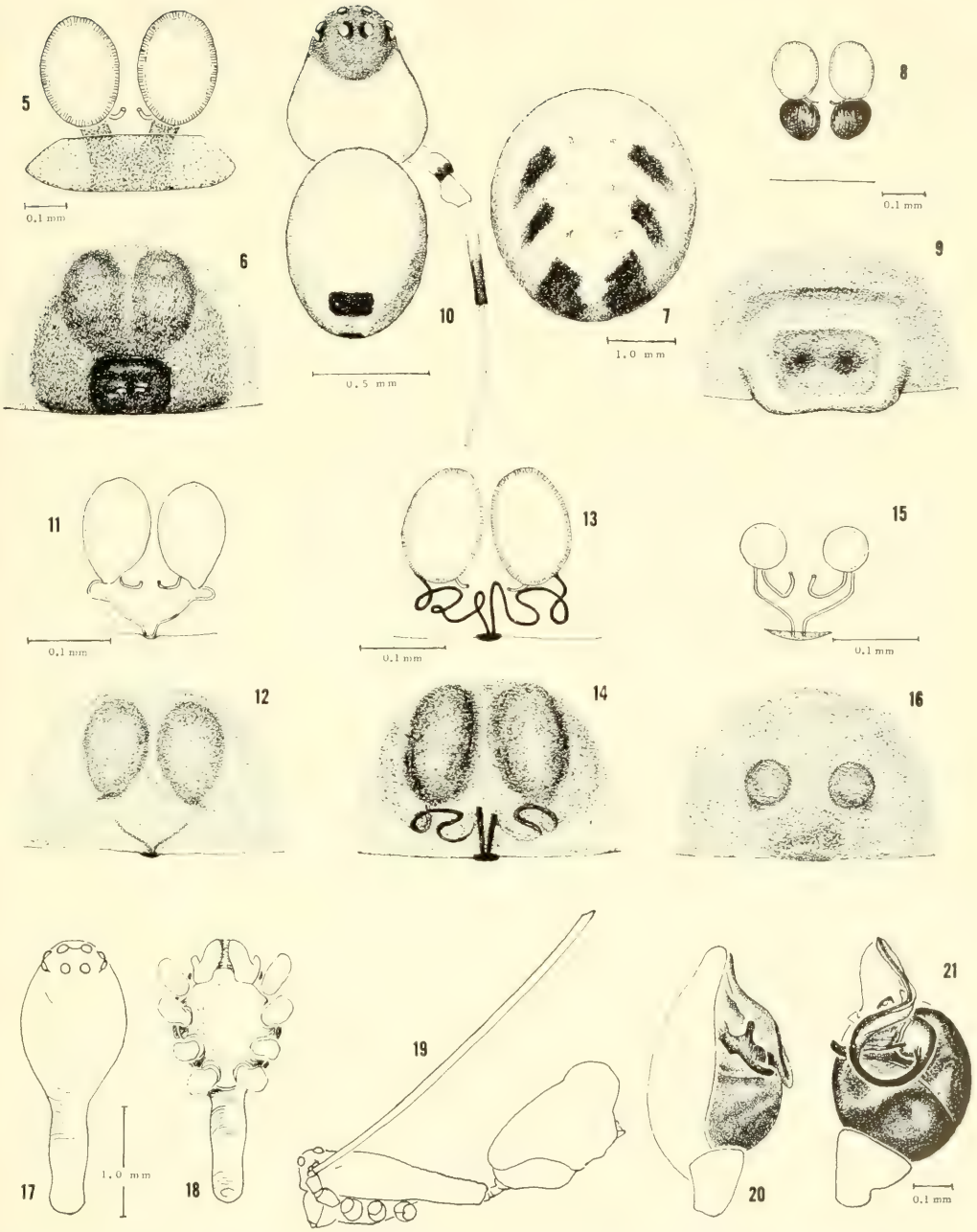
Rhomphaea altissima Mello-Leitão, 1941, Arq. Inst. São Paulo, 11:249. Female holotype from Rio Negro, Paraná, Brazil, in the Museu Nacional, Rio de Janeiro; examined.

The single specimen examined is very close to *A. projiciens*; however, it differs in having the opening of the epigynum (Fig. 37) more anterior than in any specimen of the latter species examined. Thus it is believed to belong to a separate species.

Argyrodes elevatus Taczanowski

Argyrodes elevatus Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, 9:120, pl. 5, fig. 12. Female holotype from Uassa, French Guiana [Rio Uaça, Amapa, Brazil] in the Polish Academy of Sciences; examined.—Exline and Levi, 1962, Bull. Mus. Comp. Zool., 127:134, figs. 128–132, ♀ ♂, map 5.

Conopistha friburgensis Mello-Leitão, 1943, An. Acad. Brasileira Cienc., 15:259. Female holotype from [Nova] Friburgo, [Est.] Rio de



Figures 5, 6. *Achaearanea orgea* sp. n. 5. Female genitalia, dorsal view. 6. Epigynum.
Figures 7–9. *Theridion humboldti* sp. n. 7. Dorsal view of abdomen of female. 8. Female genitalia, dorsal view. 9. Epigynum.
Figures 10–12. *Thymoites palo* sp. n. 10. Female, dorsal view. 11. Female genitalia, dorsal view. 12. Epigynum.
Figures 13, 14. *Thymoites urubamba* sp. n. 13. Female genitalia, dorsal view. 14. Epigynum.
Figures 15, 16. *Thymoites machu* sp. n. 15. Female genitalia, dorsal view. 16. Epigynum.
Figures 17–21. *Helvibis chilensis* (Keyserling). 17. Dorsal view of male carapace. 18. Male sternum, coxae and pedicel. 19. Male lateral view. 20, 21. Left palpus. 20. Mesal view. 21. Ventral view.

Janeiro, in the Museu Nacional, Rio de Janeiro; examined. NEW SYNONYMY.

Conopistha pickeli Mello-Leitão, 1943, An. Acad. Brasileira Cienc., 15:259. Female holotype from Tapera, Pernambuco, Brazil, in the Museu Nacional, Rio de Janeiro; examined. NEW SYNONYMY.

Distribution. Southern United States to Peru and Argentina, probably Chile.

Collections. This seems to be by far the most common *Argyrodes* in the webs of *Nephila* and *Argiope* in the São Paulo and Rio de Janeiro, Brazil, areas. It was also collected in the Serra dos Orgãos at 1,500 m and in the dry surroundings of Santiago del Estero, Argentina.

Argyrodes solidao sp. n.
Figures 32–34

Holotype. Female from roadside orb web, Açude da Solidao, Alto da Tijuca, Est. Guanabara, 17 April 1965 (J. Becker, H. Levi), in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the type locality.

Description. Carapace, sternum, dark brown. Legs brown. Abdomen with silver spots on black, dorsum much darker than venter, mostly black. A broad black band on posterior from the humps to the spinnerets. Anterior median eyes larger than others, one and one-half diameters apart, two-thirds diameter from laterals. Posterior median eyes two diameters apart, about one diameter from laterals. Abdomen as illustrated by Figure 34. Total length, 2.9 mm. Carapace, 1.0 mm long, 0.6 mm wide. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm. Second patella and tibia, 0.9 mm; third, 0.4 mm; fourth, 0.6 mm.

Diagnosis. The epigynum was taken off and examined by phase microscope but the exact course of the duct could not be followed. However, the loop of the duct from the opening between the seminal receptacle and the wall of the epigynum separates this species from *Argyrodes affinis* O. P.-Cambridge, and the coiled duct (Fig. 32) from those having similar epigyna.

Record. Female paratype collected with holotype.

Steatoda andina (Keyserling)

Lithyphantes andinus Keyserling, 1884, Die Spinnen Amerikas, 2(1):132, pl. 6, fig. 82, ♀ ♂. Syntypes from Junín, Amable María, Lima and San Mateo, Peru, in the Polish Academy of Sciences, Warsaw.

Steatoda andina,-Levi, 1962, Psyche, 69:26, figs. 16–19, ♀ ♂, map.

Distribution. From northern Venezuela to northern Chile.

Record. PERU. *Lima*: on loma in desert under stone, Atocongo near Pachacamac, ♀, 7 Feb. 1965. *Cuzco*: Cuzco, 3,200 m, Feb. 1965 (F. Carrasco).

Steatoda diamantina Levi

Steatoda diamantina Levi, 1962, Psyche, 69:31, figs. 28–30. Female holotype from Diamantina, Minas Gerais, Brazil, in the American Museum of Natural History.

One specimen, probably collected under bark, 33 km S of São Paulo, Brazil, differs in proportions of some soft parts of the palpus from the paratype illustrated.

Steatoda chinchipe Levi

Steatoda chinchipe Levi, 1962, Psyche, 69:32, figs. 31, 32, ♀. Female holotype from Rio Chinchipe, Cajamarca, Peru, in the Museum of Comparative Zoology.

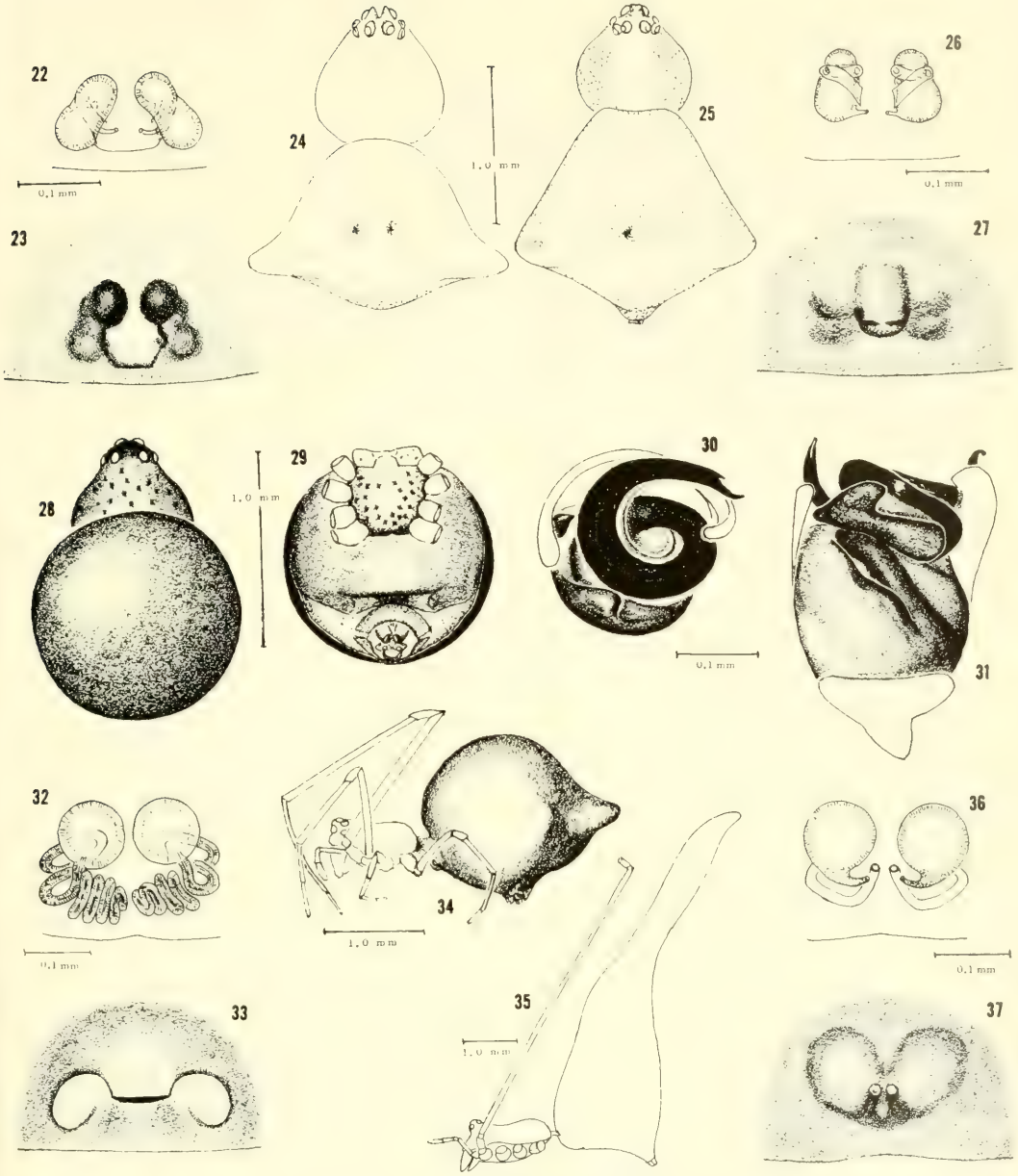
Distribution. Ecuador, Cajamarca, Junín, Peru.

Record. PERU. *Junín*: San Ramón, 800 m, in wet rain forest area, 1 ♀, Feb. 1965.

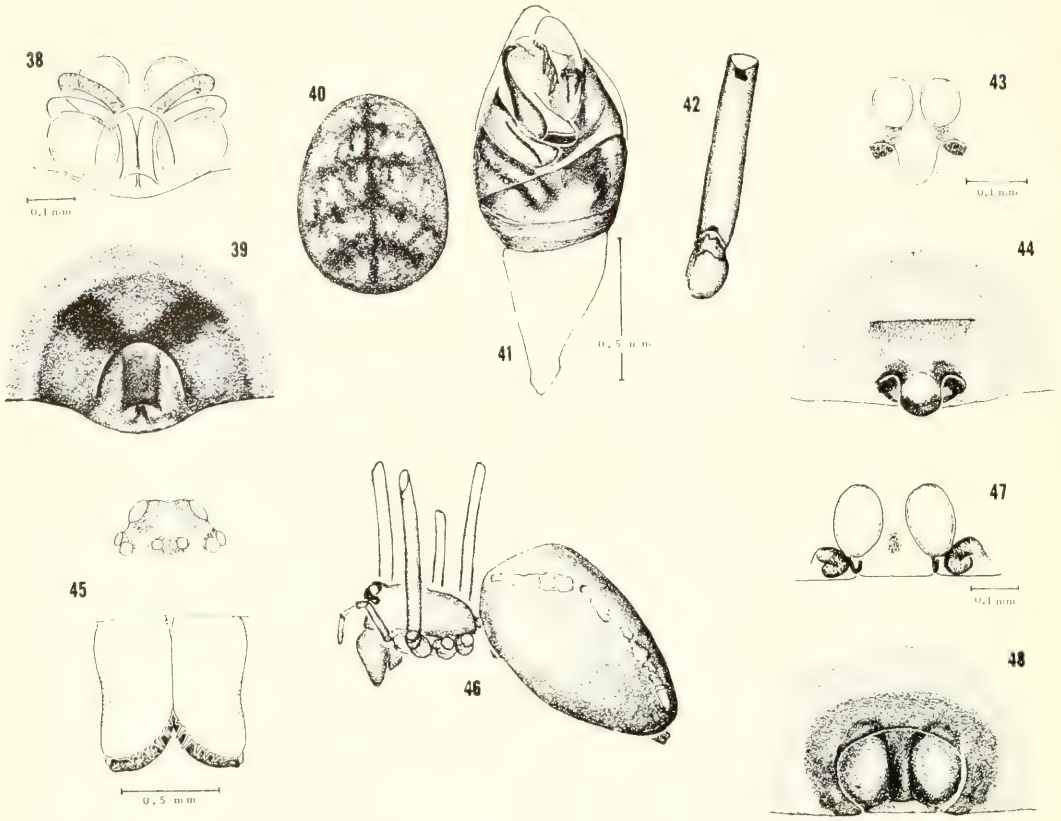
Dipoena mendoza sp. n.
Figures 38–40

Holotype. Female from Mendoza, 900 m, Province Mendoza, Argentina, 30–31 March 1965 (H. Levi), in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, dark brown. All except last coxae dark brown. Coxae of fourth legs colorless. Proximal ends of femora light, distal ends brown. Patellae brown, all other leg segments darker, with distal end darkest. Dorsum of



Figures 22–24. *Episinus rio* sp. n. 22. Female genitalia, dorsal view. 23. Epigynum. 24. Female, dorsal view.
Figures 25–27. *Episinus cuzco* sp. n. 25. Female, dorsal view. 26. Female genitalia, dorsal view. 27. Epigynum.
Figures 28–31. *Wirada tijuca* sp. n. 28. Male, dorsal view. 29. Male, ventral view. 30, 31. Left palpus. 30. Apical view. 31. Ventral view.
Figures 32–34. *Argyrodes solidao* sp. n. 32. Female genitalia, dorsal view. 33. Epigynum. 34. Female, lateral view.
Figures 35–37. *Argyrodes altissimus* (Mello-Leitão). 35. Female, lateral view. 36. Female genitalia, dorsal view. 37. Epigynum.



Figures 38–40. *Dipoena mendoza* sp. n. 38. Epigynum, cleared. 39. Epigynum. 40. Female abdomen, dorsal view.
Figure 41. *Steatoda diamantina* Levi; left palpus (São Paulo).
Figures 42–44. *Mangora fida* (Mello-Leitão). 42. Ventral view of second left femur. 43. Female genitalia, dorsal view. 44. Epigynum.
Figures 45–48. *Dubiaranea argenteovittata* Mello-Leitão. 45. Anterior view of eye area and chelicerae. 46. Female, lateral view. 47. Female genitalia, dorsal view. 48. Epigynum.

abdomen mottled gray (Fig. 40), venter uniform gray. Chelicerae half the size of clypeus. Eyes subequal in size. Anterior median eyes one diameter apart, almost touching laterals; posterior median eyes less than their diameter apart, one and one-half diameters from laterals. Abdomen ovoid in shape, widest posterior of the middle. Total length, 3.4 mm. Carapace 2.5 mm long, 2.4 mm wide. First femur, 3.5 mm; patella and tibia, 4.0 mm; metatarsus, 3.1 mm; tarsus, 1.1 mm. Second patella and tibia, 2.6 mm; third, 2.1 mm; fourth, 3.5 mm.

Diagnosis. This species differs from all other *Dipoena* by the sclerotized arch-shaped ridge on the epigynum (Fig. 39), and by the two coils (Fig. 38), one anterior to the other, between the seminal receptacles on each side.

Dipoena polita (Mello-Leitão)

Theridula polita Mello-Leitão, 1947, Papéis Avulsos, Dept. Zool., São Paulo, 8(11):127. Female holotype from Santa Cruz, Est. Paraná, Brazil, apparently lost.

The coloration, shape, and proportions of the species, particularly the black stripe on the anterior side of the first and second leg suggest that this species belongs to *Dipoena*,

not *Theridula*. Judging by the primitive illustration, it may be *D. militaris* Chickering, 1943, one of the common, widespread *Dipoena* species of South America.

MISPLACED SPECIES

LINYPHIIDAE

DUBIARANEA Mello-Leitão

Dubiaranea Mello-Leitão, 1943, Arq. Mus. Nac., Rio de Janeiro, 37:166. Type species by original designation and monotypy: *D. argenteovittata*. It had been placed in the family Theridiidae.

Dubiaranea argenteovittata Mello-Leitão

Figures 45–48

Dubiaranea argenteovittata Mello-Leitão, 1943, Arq. Mus. Nac., Rio de Janeiro, 37:167, fig. 10, ♀. Female holotype from Rio Grande do Sul, in the Museu Nacional, Rio de Janeiro; examined.

Additional description. Total length, 4.8 mm. Carapace, 1.8 mm long, 1.1 mm wide. First femur, 2.4 mm; second, 2.1 mm; third, 1.5 mm; fourth, 2.1 mm. The epigynum (Fig. 48) has an indistinct rim around a transparent raised area. The large colulus, structure of the carapace, remaining leg spines, and the structure of the chelicerae (Fig. 45) indicate that the species is a linyphiid.

ARANEIDAE

Mangora fida (Mello-Leitão), new combination

Figures 42–44

Theridion fidum Mello-Leitão, 1943, Arq. Mus. Nac., Rio de Janeiro, 37:169, fig. 13, ♀. Female holotype from Rio Grande do Sul, in the Museu Nacional, Rio de Janeiro; examined.

Additional description. Both ends of each femur have a black spot on the venter (Fig. 42). The third tibia, as in other *Mangora* species, has on its anterior surface a row of thin hairs. Total length, 3 mm. Carapace 2.4 mm long, 1.9 mm wide. First patella and tibia, 1.6 mm.

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(*Received 12 May 1966.*)

Bulletin OF THE
Museum of
Comparative
Zoology

The Tertiary Lorisiform Primates of Africa

GEORGE GAYLORD SIMPSON

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 3
SEPTEMBER 29, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

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Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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INTRODUCTION

Primitive primates, prosimians in a broad sense (including tarsioids), were abundant in the early Tertiary of North America and Europe. Many of them are clearly extinct side branches without special relationships to any living forms. Others seem to be close to the ancestry of the Recent Lemuriformes and Tarsiiformes, although annectant middle and late Tertiary forms are not known. Special affinities of known early Tertiary prosimians with the Lorisiformes have been suggested but not clearly demonstrated. A single, poorly known lorisiform of probable Pliocene (Nagri) age has been described from the Siwaliks of India: *Indraloris lulli* Lewis, 1933. All other fossils definitely identified as Lorisiformes or Lorisidae (including Galaginae) are from East Africa. A few specimens are from the Pleistocene of Olduvai, Tanganyika, and belong near or in *Galago senegalensis*, a living species of the same general region. They have been discussed elsewhere (Simpson, 1965). Specimens from the Miocene of Kenya and Uganda are more numerous and taxonomically varied. They are the subjects of the present study.

The first of these specimens were discovered at Koru, Kenya, by Dr. A. T. Hopwood in 1931 for the British Museum (Natural History). Those specimens, described below, have not hitherto been mentioned in print. The first published specimen was from Songhor, Kenya, and was named *Progalago dorae* by MacInnes (1943). Many more specimens were later found by Dr. L. S. B. Leakey and his associates at Songhor and also at several localities on Rusinga Island in Lake Victoria, Kenya. Most of these were described by Sir Wilfrid E. Le Gros Clark and Mr. D. P. Thomas (1952), who referred the specimens in their hands to three species of *Progalago*. In 1956 Le Gros Clark added a description of a nearly complete skull, identified as *Progalago* sp., from Rusinga Island. A palate and facial skull from Napak, Uganda, has most recently been described as *Mioeuoticus bishopi* by Leakey (in Bishop, 1962). Other specimens are

now known that were not included in any of those previous studies, and a revision involving all materials now available is here presented.

Recent forms directly available for comparison in the Museum of Comparative Zoology, Harvard University, include all the genera and species recognized as valid by Hill (1953) with the exception of *Euoticus* [or *Galago*] *inustus*, the status of which is quite uncertain. In any event, the Miocene and Recent groups are sufficiently distinct that comparisons at the specific level are not particularly significant.

ACKNOWLEDGMENTS

This study was begun in the Coryndon Memorial Museum, Nairobi, Kenya, and completed in the Museum of Comparative Zoology, Harvard University. I am indebted to both museums for facilities and assistance. My visit to Africa and much of the work on this project were made possible by a John Simon Guggenheim Memorial Foundation Fellowship. The study was suggested by Dr. L. S. B. Leakey, and he has encouraged and aided the work throughout. Dr. Leakey and the Coryndon Memorial Museum also made possible visits to the principal field sites. Recent specimens for comparison were mainly those in the Museum of Comparative Zoology, facilitated by the Curator of Mammals, Miss Barbara Lawrence. The illustrations were drawn by Arnold Clapman at the expense of National Science Foundation grant No. GB-500. The British Museum (Natural History), Department of Geology, Dr. E. I. White, Keeper, loaned certain specimens, here involved, to Dr. Leakey. Dr. W. W. Bishop made available the type of *Mioeuoticus leakeyi*, from Napak, Uganda. (Some other specimens from Uganda and Kenya were submitted, but are not included here because they proved not, or not clearly, to be prosimian.)

This study was completed in February, 1965, and was originally intended for inclusion with studies of higher fossil primates by Dr. Leakey. To avoid delay, it is now published separately with Dr. Leakey's acquiescence.

RECENT LORISIDAE

The fossil lorisids must be compared in the first instance with the Recent forms, which are therefore briefly reviewed. The Recent Lorisiformes seem beyond serious question to comprise a valid phylogenetic taxonomic unit of rather closely related groups. They have commonly been placed in the single family Lorisidae, and I prefer to continue that usage although, inevitably, some students have split them into two or more families, usually Lorisidae and Galagidae as by Hill (1953). Those two subsidiary lorisiform taxa are here recognized as subfamilies, Lorisinae and Galaginae, of the Lorisidae.

Although they retain many primitive features and are prosimian in evolutionary level, the lorisids as a whole also have definite specializations in comparison with the earliest or with the most primitive living primates. Among these specializations are: great enlargement of orbits and correlated remodeling of facial skull but without marked absolute reduction of snout; complete bulla incorporating the ectotympanic in its lateral part; inflation of the mastoid; reduction of incisors to two and of premolars to three in each jaw; presumed lower canine incisiform and forming with the incisors the so-called "comb"; P_2 caniniform; molars essentially primitive but strong hypocone on M^{1-2} and no distinct paraconid on M_{1-3}; first digit of manus and pes extremely divergent, second usually reduced and fourth usually longest, grasping mainly between first and fourth.

The long-standing distinction of lorisines and galagines in classifications has been based primarily on these characters: the more elongate hind legs, notably in the tarsus, of the galagines; correlated loco-

motion, saltatory in galagines and hand-over-hand in lorisines; and the much more active behavior of galagines. (This is an unusual example of the diagnostic use of a behavioral character.) Classification of the fossils must, however, be based on skulls, jaws, and dentitions for the present, at least. Various authorities, especially Gregory (1922) and Hill (1953), have compared these parts in the Recent members of the two groups. Among the supposed distinctions are the following:

Lorisinae	Galaginae
Cranium less globular; posterior part flattened dorsoventrally.	More globular; not flattened.
Bulla and mastoid inflation variably less; mastoid projects laterally.	Strongly inflated, but mastoid projects less laterally.
Zygoma and mandible deep, heavy.	Slender.
Orbits directed more forward or forward and upward.	Orbits directed more laterally.
Interorbital septum narrower.	Wider.
Palate and dental arch broader and shorter.	Narrower and relatively longer.
Basicranial region shorter, midcranial longer.	Midcranial shorter, basicranial longer.
Skull shorter and wider.	Skull longer and narrower (but cranium relatively broader, *fide* Hill).
P_4^4 relatively shorter, not molariform.	P_4^4 submolariform; P_4 elongate with well developed talonid.

I cannot confirm any single skull character as typologically diagnostic, that is, as affording a clear-cut distinction between all the members of one subfamily and all of the other. Evidence of pertinence to a subfamily may, nevertheless, be given by characters that do appear in some members of a subfamily, although not in all, and that do not occur in the other subfamily. For example, a relatively uninflated bulla, flattened ventrally, and a deep, heavy mandible occur in some Lorisinae (in *Perodicticus* and to some extent in *Nycticebus*, but not in *Loris* or *Arctocebus*) and in no Galaginae. I have been unable to confirm some supposed distinctions in any members of the pertinent subfamilies. For example, Hill (1953) gives cuspidate cingula on upper incisors and a long upper post-canine diastema as characteristic of Galaginae (his Galagidae), but I did not find these features on any specimens seen by me and they are absent in Hill's own illustrations.

The only character of skull and dentition that I have found to be typologically diagnostic of the Recent subfamilies is the greater molarization of the premolars in the Galaginae. Even this character must be evaluated with caution when dealing with fossils. In the first place, in this family dm_4^4 are not lost until well after M_3^3 are in full use. An apparent adult with seemingly molariform P_4^4, diagnostic of the Galaginae, may therefore in reality be a young lorisine retaining molariform dm_4^4. In the second place, the Recent lorisine condition is presumably primitive and probably occurred at some time in the galagine ancestry. And finally, any single character such as this may not stand up among all extinct lineages. There is no *a priori* reason why some Tertiary lorisine might not have evolved more specialized P_4^4 as in Recent galagines.

Under these circumstances, reference of fossils to the Lorisinae, Galaginae, or neither cannot be based on typological definitions

of subfamilies but, if possible at all, depends on balances of resemblances and on possible phylogenetic connections with one or another of the living species and genera.

Four species of living lorisines are now generally recognized, and these are so distinct that they are almost always placed in four monotypic genera: *Loris tardigradus*, *Nycticebus coucang*, *Arctocebus calabarensis*, and *Perodicticus potto*. The geographic associations and the vernacular naming of the first two species as "lorises" and of the latter two as "pottos" belie their resemblances and probable affinities. Asiatic *Loris* most closely resembles African *Arctocebus*, and Asiatic *Nycticebus* African *Perodicticus*. The resemblances might conceivably be convergent, but it seems more likely that they are homologous. It is probable that the two ancestral *Loris–Arctocebus* and *Nycticebus–Perodicticus* lineages first became differentiated and that in each a geographically isolated, vicarious pair of species and genera later evolved in Asia and Africa.

Although the Galaginae include more species than the Lorisinae, they are a more compact group, no two of them differing as much as do, for example, *Loris tardigradus* and *Perodicticus potto*. Five species of living galagines are universally recognized and one or two more may prove valid although now defined inadequately, at best. With the inflationary taxonomy that afflicts all the primates, each of the five sure species has been given generic rank at one time or another, but all have also been placed in the single genus *Galago*. Hill (1953) recognizes *Galago* with the species *senegalensis* (type), *crassicaudatus*, and *alleni*, *Euoticus elegantulus*, and *Galagoides demidovii*. Dentally and osteologically, at least, the last named species seems quite close to the type of *Galago*, and I prefer to leave it in that genus, recognizing only the slightly more aberrant *Euoticus elegantulus* as generically distinct. Hill also recognizes a sixth supposed species, *Euoticus inustus*, the only species here named that I have not seen. It was first described as a subspecies of *Galago senegalensis*, which may yet prove to be its correct status, but was given specific rank and removed to *Euoticus* on the grounds that the nails are somewhat pointed and ridged as in that genus. That single character seems inadequately definitive, and it is possible that it occurs as a specific, subspecific, or indeed merely individual variation in *Galago*.

There is no evidence that galagines have ever occurred outside of Africa, where they seem to represent moderate radiation of a single stock. They superficially resemble *Tarsius*, and may be considered the Ethiopian vicars of the Oriental tarsiers, but in this case it is clear that the resemblance is convergent.

Although the Recent species, as here listed (with the probable exception of "*Euoticus inustus*"), can be readily identified from skulls and dentitions, all are markedly variable. Not even the dental formula, variations in which are often considered by paleontologists as *ipso facto* generic, is constant. For all species the modal formula, in the customary form, is indeed $\frac{2\cdot1\cdot3\cdot3}{2\cdot1\cdot3\cdot3}$, as given in all the reference works, but deviations from it are so common that they cannot be considered abnormal. The small Museum of Comparative Zoology series of lorisines includes a skull of *Nycticebus coucang* with a single pair of upper incisors and no trace of others, as well as one of *Perodicticus potto* with no trace of M^3 on either side and indeed no place for those teeth in the alveolar margin. There is also a skull of *Galago crassicaudatus* that has the normal two incisors on one side but on the other side a single tooth with a bifid crown, as if the two incisors had fused in the alveolar direction and formed a single crown base and root. Variations of each of the teeth in size and structural details are also striking, and they become spectacular in M^3 of *Perodicticus potto*, which may be only moderately smaller than M^2 and similar in structure,

may be a vestige with only one distinct cusp, or may be entirely absent.

Finally, a comment should be made on the dental formula. It is generally assumed that the teeth present, in terms of those primitive for placentals, are I^{1-2}_{1-2} C^{1}_{1} P^{2-4}_{2-4} M^{1-3}_{1-3}. However, I do not know of any conclusive evidence that the third tooth in the lower jaw, completely incisiform, is not in fact an incisor, in which case the lower canine has been lost. It is also uncertain which upper or, if any, which of the original three lower incisors and which of the original four premolars have been lost. The gap in the upper series is in the position of I^{1}, not I^{3}. The most anterior of the remaining lower premolars occludes directly against the posterior side of the upper canine, and this seems more likely for P_1 than for P_2. If this tooth is P_1, P_2 is probably the one that is absent. The teeth really present may be I^{2-3}_{1-3} C^{1}_{0} $P^{2-4}_{1,3-4}$ M^{1-3}_{1-3}. Nevertheless, to avoid confusion in comparison with other literature, I here use the conventional identifications, and they may finally prove to be correct.

LOCALITIES AND AGE

Collections in Kenya were made by L. S. B. Leakey and his associates, for the most part from 1947 to 1956, at Songhor and on Rusinga Island. Songhor is in Kericho approximately 31 miles almost due east of Kisumu. Rusinga Island, South Nyanza, is at the mouth of Kavirondo Gulf, 40–45 miles west-southwest of Kisumu. The few specimens from near Koru were found in 1931 by A. T. Hopwood. The Koru locality, in Kericho, is about eight miles south-southeast of Songhor. All three Kenya localities are shown, e.g., in Whitworth, 1954, fig. 1, and on War Office map G.S.G.S. 4355, Sheet S.A. 36/3 (the Kisumu sheet of the map of East Africa on the scale 1:500,000). The Songhor and Koru specimens are from essentially unified deposits of small extent. Those from Rusinga Island are scattered over a large area and in a thick and complex sequence of beds. The more precise field localities of the various Rusinga specimens are given below as far as available. Those localities are mapped and approximately placed stratigraphically in Whitworth, 1954, figure 2, and page 4. The geology of Rusinga Island and adjacent areas is further discussed by Shackleton (1951), Whitworth (1953), and McCall (1958).

The one identifiable specimen (*Mioeuoticus*) from Uganda is from the dissected Tertiary volcano Napak in Karamoja, northeast Uganda, or more exactly from faunal site Napak I in a col between Akisim and Alekilek. The geology is discussed and a detailed map is given by Bishop (1962).

At all four localities the lorisiforms are accompanied by higher primates and by numerous mammals of other orders. Complete faunal lists are not yet available for any of the localities. It seems highly improbable that all parts of the complex Rusinga sequence and the other three widely scattered deposits are of the same geological age. The incomplete yet rather extensive faunal studies so far made have not, however, established any appreciable difference in age or any determinable sequence either within the Rusinga complex or among the four localities. The lorisiforms so far have no significance in this respect. As shown in Table 1, they are not quite the same at the four localities, but the differences could be due entirely to chances of discovery or to differences of facies, for which there is some other evidence (see Whitworth, 1958, pp. 45–47). In any event, they do not in themselves suggest a temporal sequence.

Data for correlation of these faunas with the standard European stages are exiguous. An early suggestion that they are Burdigalian is frequently repeated and has come to seem authoritative by mere repetition. Nevertheless, it rests on minimal, inconclusive, and in part conflicting evidence. The broader, even more frequently repeated statement that these deposits are Lower

Table 1. Localities of identified specimens of Tertiary lorisids; mandibles only

	Rusinga					Songhor	Koru
	R1a	R2	R3a	Kathwanga	Gumba		
Progalago dorae	×					×	
P. songhorensis						×	
P. cf. *songhorensis*				×			
Komba robustus			×		×	×	
K. cf. *robustus*		×					×
Komba minor	×					×	
Propotto leakeyi	[Probably also Rusinga, site uncertain]					×	

Miocene depends not only on their uncertain correlation as Burdigalian but also on the placing of the Burdigalian itself, considered Lower Miocene by some authorities but Middle Miocene by others.

Recently, Evernden, Savage, Curtis, and James (1964) have reconsidered the age of the Rusinga deposits on the basis of potassium/argon ratios and also (at second hand) the faunas. They conclude that the age is Barstovian in American terms, which would be Vindobonian (in a broad sense, at least) in European terms. Most stratigraphers would call that late Miocene although some might consider it middle Miocene. In their sample data, Evernden *et al.* confusingly give the age of their Rusinga rock samples as "Early Miocene (?), Early Pliocene (?)." The radiological date was arrived at by selecting one of five radically discrepant results. Three are obviously wrong. Another, although discarded, would place the beds in the Burdigalian, which has long been considered probable on other grounds. Their selected date indicates little or no difference in age from beds at Fort Ternan where the fauna is clearly and decidedly later. Their conclusion on radiological grounds is unconvincing, at best.

The paleontological evidence of these authors is even less convincing. The record really most suggestive of middle or late Miocene age is perhaps *Dorcatherium*, which is predominantly Vindobonian in Europe. However, contrary to their Table 7, the genus has been reported from the Burdigalian. The African forms are, moreover, distinctive and might well represent pre-Vindobonian origin of the genus in Africa or an allied but earlier genus. Aside from that, Evernden *et al.* emphasize "a number of forms . . . never . . . reported previously in early Miocene deposits," but without exception these are groups with such scanty fossil records that they could just as well turn up in the early Miocene as anywhere else. The authors include galagines in this supposed evidence for post-early Miocene age, but in fact (as their own Table 7 shows) no fossil galagines have been reported from any other deposits. They have at present no bearing whatever on the age of these beds within the Cenozoic. This is not the place to discuss the correlation further, and the data for doing so are not yet adequate. It must, however, be emphasized that the fossils described here do *not* help in this respect. In themselves they do not suggest any particular age, and the indirect evidence at present hardly warrants greater precision than to say that they are probably Miocene.

CONSOLIDATED SPECIMEN LIST

Specimens collected by Leakey's parties generally have field designations including a symbol for the area of collection, the serial number for the season, and the year, marked on the specimens themselves in India ink. Thus S10'49 indicates the tenth specimen collected at Songhor in 1949. Most of the specimens described by Le Gros Clark and Thomas (1952) were given their field designations, only, in slightly

different form, S10'49, for example, being published by them as S.10, 1949. Other field designations have R for Rusinga Island. The types, only, of three species previously recorded from Kenya were deposited in the British Museum (Natural History) where they were given numbers in the register of fossil mammals (indicated by the prefix or superscript M). Thus the type of *Progalago dorae*, S9'38, is also B.M. (N.H.)M. 16907, and is so listed by Le Gros Clark and Thomas. Specimens not in the British Museum are, with few exceptions, in the Coryndon Memorial Museum, Nairobi, Kenya. Almost all the primate specimens of the Leakey collections, including some already registered with British Museum (Natural History) numbers, were there listed and numbered in a special manuscript catalogue of fossil primates. Thus the type of *Progalago minor* has the number 103 on the specimen itself (for S103'48), is described as Brit. Mus. (Nat. Hist.) M. 16877 by Clark and Thomas, but has the Coryndon Memorial Museum (hereafter abbreviated C.M.M.) primate catalogue number 297. The latter numbers have not hitherto been used in publication, but are useful for finding and identifying the specimens at C.M.M. The two specimens from Koru have British Museum numbers, only, and the one specimen from Napak has both a field number and a registry number (NAP. I.3.6/58) given by Bishop (1962) in the original publication.

Completeness of reference to previous literature and existing collections and archives thus involves five different systems, with at least two distinct designations for each specimen in most cases and sometimes three. Repeated complete listing in text, tables, and legends of illustrations would be almost impossibly clumsy. There is also some convenience in having data on all specimens given just once in a consolidated list. I therefore give such a list in this section along with irreducibly short and simple letter designations (A, B, etc.) which will be used throughout the rest of this study. Although still another set of specimen designations is thus added, this reduces the complication and confusion that would ensue from attempts to use those already applied. Available locality data, reference to previous publications (if any), and notes as to anatomical parts preserved are given in this list and not repeated elsewhere.

There are no instances of association of skull and mandible or upper and lower teeth. Those two categories of specimens are therefore listed separately. The classification is at present based primarily on lower dentitions, and they alone figure in the distribution data of Table 1.

Lower Jaws and Teeth

Progalago dorae

A. Type. S9'38; C.M.M. 100; B.M.(N.H.) M. 16907. Left ramus: P_4, M_2; alveoli P_3, M_1, M_3. MacInnes, 1943, pp. 145–148, pl. 23, figs. 2, 2A, 2B. Clark & Thomas, 1952, p. 2, pl. 2, figs. 4, 5.

B. R608'49; C.M.M. 370. Left ramus: M_1 (broken), M_2, M_3 (broken); alveoli $P_{2\text{–}4}$. Clark & Thomas, 1952, p. 5. Site R1A.

C. S310'49; C.M.M. 404. Right ramus: $P_{2\text{–}4}$. Clark & Thomas, 1952, pp. 3–4, pl. 3, fig. 6.

D. S104'48; C.M.M. 298. Right ramus: $P_{2\text{–}3}$; alveoli P_4–M_3. Clark & Thomas, 1952, p. 4.

Progalago songhorensis

E. Type. S10'49; C.M.M. 388. Left ramus: $M_{2\text{–}3}$. Clark & Thomas, 1952, pp. 4–5, pl. 3, figs. 7–8 (as "*Progalago dorae*").

F. S81'47; C.M.M. 206. Left ramus: M_2 (broken), M_3. Clark & Thomas, 1952, p. 5.

P. cf. *songhorensis*

G. R167'51; C.M.M. 625. Left ramus: P_3–M_1 (all broken); alveoli I_1–P_2. Clark & Thomas, 1952, pp. 5–6, text-fig. 1 (as "*Progalago dorae*"). Kathwanga.

Komba robustus

H. Type. S390'49; C.M.M. 414; B.M.(N.H.) M. 16876. Right ramus: P_3 (broken), P_4–M_2; alveoli I_2–P_2. Clark & Thomas, 1952, pp. 9–10, pl. 3, figs. 14, 16 (as "*Progalago*" *robustus*).

I. S102'48; C.M.M. 296. Left ramus: P_4–M_2; alveoli P_3. Clark & Thomas, 1952, pp. 10–11 (as "*Progalago*" *robustus*).

J. S8'47; C.M.M. 194. Right ramus: M_3; alveoli M_2. Clark & Thomas, 1952, p. 11, pl. 3, fig. 12 (as "*Progalago*" *robustus*).

K. R76'51; C.M.M. 621. Right ramus: M_{1-2} (all imperfect). Site R3a.

L. R618'50; C.M.M. 544. Right ramus: M_{1-3}. Clark & Thomas, 1952, p. 10, pl. 3, fig. 15 (as "*Progalago*" *robustus*). Site Gumba.

K. cf. *robustus*

M. R278'56; C.M.M. 717. Right ramus: M_{2-3}. Site R2.

N. B.M.(N.H.) M. 14282. Right ramus: P_4–M_2. Collected by A. T. Hopwood at Koru, 1931.

?*Komba minor*

O. Type. S103'49; C.M.M. 297; B.M.(N.H.) M. 16877. Right ramus: M_{1-3}. Clark & Thomas, 1952, pp. 11–12, pl. 3, figs. 17–18 (as "*Progalago*" *minor*).

P. S458 (no other date). Left ramus: P_4–M_2.

Q. R611'49; C.M.M. 371. Left ramus: M_{1-3}. Clark & Thomas, 1952, p. 12 (as "*Progalago*" *minor*). Site R1a.

Propotto leakeyi

R. Type. S391'49; C.M.M. 421A. Right ramus: P_3–M_2, alveoli of M_3.

S. SONGHOR. (The locality "Songhor," without field number or year of collection, is lettered on the specimen; the label with the specimen belongs to an upper molar from Rusinga 1 and is incorrect.) Left ramus: P_3–M_1, M_3, alveoli of M_2.

T. 1'58; C.M.M. 745. Right ramus: M_{2-3}, roots of P_4–M_1. (Site not definitely entered but probably Rusinga.)

Lorisidae indet.

U. R649'49; C.M.M. 372. Isolated tooth. Site "Kanugere beyond R3a." This closely resembles a galagine left P_2 and was identified as that tooth of *Progalago dorae* by Clark & Thomas, 1952, p. 4. It is, however, too large to belong to that species and it cannot be definitely ascribed to any of the forms here described.

V. R516'49; C.M.M. 358. Site R3a. An isolated P_2 (not in bone) could belong to *Progalago dorae*, to which it was referred by Clark & Thomas, 1952, p. 4. In my opinion the tooth does not suffice for positive identification. Under the same field and catalogue number but almost certainly not of the same individual is a bone fragment with the talonid of M_1 or M_2. This is inseparable from *Komba robustus*, although it does not suffice for positive identification.

SKULLS AND UPPER TEETH

Cf. *Progalago dorae*

AA. R1'54; C.M.M. 702. Nearly complete skull, with right P^3–M^3 and left M^1–^{3}, and alveoli of all other teeth. Le Gros Clark, 1956, pp. 1–6, pl. 1. Site R106B (west of R106). (Although given a 1954 field number, the specimen was found in 1952.)

AF. S93'48; C.M.M. 291. Fragment of right maxilla with roots of lateral incisor and canine and crowns of P^{2-3}. Clark & Thomas, 1952, p. 7, pl. 3, fig. 9.

Cf. *Progalago songhorensis*

AE. B.M.(N.H.) M. 14301. Fragment of left maxilla with M^{1-3}. Collected by A. T. Hopwood, 1931, at Koru.

AG. S391'49; C.M.M. 421B. Fragment of left maxilla with M^2.

AH. S22'49; C.M.M. 400A. Fragment of left maxilla with P^4 and remnants of M^{1-2}.

Cf. *Komba robustus*

AB. R279'56; C.M.M. 718. Fragment of left maxilla with P^4–M^2. Site R2.

AC. R106'48; C.M.M. 219A. Fragment of left maxilla with M^{2-3}. Clark & Thomas, 1952, p. 6, pl. 3, fig. 10. Site R106.

AD. R1005'50; C.M.M. 555. Cranial part of skull with much of endocast exposed; no teeth. Clark & Thomas, 1952, p. 14, pl. 1, figs. 1–2; pl. 2, fig. 3. Site R3.

Lorisine indet.

AI. S643'56 (no C.M.M. number). Fragment of right maxilla with broken M^2.

Miocuoticus bishopi

AJ. Field No. 3'58; registry number NAP. I.3.6/58. This specimen is part of a collection made by W. W. Bishop for the Geological Survey of Uganda. There was an understanding that type material from that collection would eventually be lodged in the British Museum (Natural History). Facial part of skull with right P^2 and P^4–M^2, left P^4–M^3, and roots of other teeth. The original description (Leakey in Bishop, 1962, p. 7) states in one place that right and left P^4 are missing but later says correctly that they are present and describes them. Described under the foregoing registry number by L. S. B. Leakey as type of *Miocuoticus bishopi* in Bishop, 1962, pp. 6–8, pl. 3, figs. A, B, D.

CLASSIFICATION AND DESCRIPTION OF LOWER JAWS AND DENTITIONS

As far as the specimens from Kenya are concerned, formal classification is based on lower jaws and dentitions. They are more numerous than parts of skulls and upper dentitions; they fall more clearly into groups now definable; and the types of the three

Table 2. Identifications by Le Gros Clark and Thomas, 1952, and in present work

Designation in present consolidated list	Identification by Le Gros Clark and Thomas	Present identification
A	*Progalago dorae*	*Progalago dorae*
B	*Progalago dorae*	*Progalago dorae*
C	*Progalago dorae*	*Progalago dorae*
D	*Progalago dorae*	*Progalago dorae*
E	*Progalago dorae*	*Progalago songhorensis*
F	*Progalago dorae*	*Progalago songhorensis*
G	*Progalago dorae*	*Progalago* cf. *songhorensis*
H	*Progalago robustus*	*Komba robustus*
I	*Progalago robustus*	*Komba robustus*
J	*Progalago robustus*	*Komba robustus*
L	*Progalago robustus*	*Komba robustus*
O	*Progalago minor*	*Komba minor*
U	*Progalago dorae*	Lorisid indet.; not *P. dorae*
V	*Progalago dorae*	Lorisid indet.; inseparable from *P. dorae*
AC	*Progalago dorae*	cf. *Komba robustus*
AD	*Progalago* sp.	cf. *Komba robustus*
AF	*Progalago dorae*	cf. *Progalago dorae*

species previously established are all parts of lower jaws. Le Gros Clark and Thomas had no specimens of the very distinctive form here named *Propotto leakeyi*. They conservatively placed all the specimens available to them in the genus *Progalago* and most of them in the first species to be named, *P. dorae*. It now seems that at least two genera are present and also that their *P. dorae* embraced two closely allied but distinguishable species. The lorisid fauna is more varied than then appeared, and a further result is that some fragmentary specimens then reasonably placed in *P. dorae* do not now seem to be definitely identifiable. Reference to the work of Le Gros Clark and Thomas, which retains its value and of course is not repeated here, is facilitated by Table 2, giving their identifications and those now proposed for all the specimens known to them.

Family LORISIDAE Gregory, 1915

Under the latest (1961) International Code of Zoological Nomenclature this name might be ascribed to Gray, 1821, or perhaps to a still earlier author who used any term (even vernacular) for the "family group." I urge reasonable adherence to those rules, but cannot bring myself to give as authority for a name an author who did not, in fact, use it.

As mentioned in the summary of Recent forms, all the living lorisiforms, both lorisine and galagine, are here referred to this one family. The family thus broadly construed clearly also embraces all the known fossil lorisiforms. Their possible closer relationships are discussed in a later section, where it will be shown that *Propotto* is lorisine. *Indraloris* may be lorisine on equivocal and indirect evidence, and *Progalago* and *Komba* are uncertain as to subfamily.

PROGALAGO MacInnes

Type-species: *Progalago dorae* MacInnes.

Progalago MacInnes, 1943, p. 145.

Known distribution: Miocene of Kenya: Rusinga Island and Songhor.

Diagnosis (emended from MacInnes, 1943, and Clark and Thomas, 1952): Lorisids with dental formula and general aspect of dentition as in the Recent genera. P_4 (known in *P. dorae* only) oblique; trigonid almost unicuspid, faint indication of metaconid; talonid large, broad, basined, with elevated, cuspidate rim but cusps not prominent. Molars with low, relatively bunodont cusps; trigonids and talonids of about equal height; trigonids very short proximodistally, subquadrate, without anterobuccal cuspule. M_3 averaging more elongate than in Recent galagines. Mandible deep under M_3.

Discussion: MacInnes based this genus on a single specimen and defined it as having a unicuspid P_4 and deep ramus under M_3. P_4 of his specimen is worn. When unworn it is indeed distinctive but more complex than MacInnes could realize, as shown by specimen C of my consolidated

list, carefully described by Clark and Thomas (1952, pp. 3–4). Clark and Thomas also deleted from the diagnosis the depth of the mandible, but that was in order to include the two species that are here removed to the new genus *Komba*. So far as now appears, the depth of mandible noted by MacInnes is a generic character of *Progalago*. Specimens hitherto referred to *P. dorae* demonstrably fall into two groups, here defined as separate species.

Progalago dorae MacInnes

P. dorae MacInnes, 1943, p. 145.

Holotype: Specimen A of consolidated list.

Hypodigm: Specimens A, B, C, and D. A doubtfully referred skull, AA, is not included in the technical hypodigm.

Known distribution: Miocene of Songhor and Rusinga R1a, Kenya.

Diagnosis (new): Larger than *P. songhorensis*. M_2 more rounded. Molar trigonids relatively short and talonids expanded. No external cingulum on trigonids. Measurements of lower teeth as in Table 3.

Discussion: MacInnes' diagnosis was not differential, no other species of *Progalago* being then known. Clark and Thomas (1952) gave a diagnosis differential with respect to their *Progalago robustus* and *minor*, here removed from this genus. They cited the deep mandible and the size [larger than *robustus* and *minor*]. The "weakly developed external cingulum on the anterior part of the lower molars" does not occur in the type and is now considered characteristic of a second species, *P. songhorensis* (below). Other characters given in Clark and Thomas' diagnosis, not very distinctive in any case, were derived from upper molars (specimen AC) which, in my opinion, probably do not belong to this species or genus.

The specimens now placed in this species were all known to Clark and Thomas. Their descriptions and figures plus the present new measurements and figures suffice without further detailed comment.

Progalago songhorensis[1] new species

Holotype: Specimen E of consolidated list.

Hypodigm: Specimens E and F. Specimen G is referred with doubt.

Known distribution: Miocene of Songhor and doubtfully Kathwanga on Rusinga Island.

Diagnosis: Smaller than *P. dorae*. M_2 somewhat more angular. Molar trigonids slightly longer, relatively, and talonids slightly less expanded. External cingulum on trigonid. Measurements of lower teeth as in Table 3.

Discussion: This species closely resembles *P. dorae*, and the specimens now placed in it were referred to *P. dorae* by Clark and Thomas. Comparison is based mainly on four specimens with M_2 (specimens A and B of *P. dorae*; E and F of *P. songhorensis*). The size difference is greater than one would expect in a single species, as judged by comparison with Recent lorisids, in which M_2 is less variable than, for example, M_3. The difference in size is also consistently associated with the several morphological differences noted in the diagnosis. It cannot be maintained that two species are certainly present, but the probability is so great that formal separation seems justified.

Specimen G, also referred to *P. dorae* by Clark and Thomas, is smaller than any specimens now considered certainly *P. dorae* and is more nearly the size of *P. songhorensis*. It may be even a bit smaller than typical *P. songhorensis*, and reference to *Komba robustus* (a still smaller species despite its name) is possible but unlikely. Direct comparison with specimens confidently referred to *P. songhorensis* is impossible because none have the teeth present in G.

Specimen G is of special interest because it preserves parts of the broken alveoli of the teeth usually (but perhaps incorrectly) identified as I_{1-2} C and P_2 in lorisids and

[1] Locative form of Songhor, the type locality.

TABLE 3. MEASUREMENTS IN MILLIMETERS OF LOWER TEETH OF MIOCENE LORISIDAE FROM KENYA. Designations of specimens (A, B, etc.) refer to the consolidated specimen list, where other data are given. In each species, the first specimen listed is the type. L, length (proximo-distal). W, width (bucco-lingual). Measurements taken to 0.1 mm with calibrated reticle in binocular microscope.

Identifications and specimens	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
Progalago dorae										
A	–	–	3.4	2.1	–	–	3.7	3.4	–	–
B	–	–	–	–	–	–	4.0	3.4	*ca.* 5¼	–
C	3.1	1.9	3.5	2.2	–	–	–	–	–	–
D	3.4	1.8	–	–	–	–	–	–	–	–
Progalago songhorensis										
E	–	–	–	–	–	–	3.3	2.7	3.9	*ca.* 2½
F	–	–	–	–	–	–	3.5	2.9	4.4	2.7
Progalago cf. *songhorensis*										
G	*ca.* 2½	–	*ca.* 2½	–	*ca.* 3	*ca.* 2½	–	–	–	–
Komba robustus										
H	–	–	2.6	1.6	2.8	2.2	2.9	2.3	–	–
I	–	–	2.3	1.8	2.8	2.3	2.7	2.4	–	–
J	–	–	–	–	–	–	–	–	3.5	2.1
K	–	–	–	–	–	–	2.8	2.1	3.1	2.0
L	–	–	–	–	2.9	2.5	3.0	2.5	3.7	2.3
Komba cf. *robustus*										
M	–	–	–	–	–	–	2.9	2.0	3.4	2.0
N	–	–	2.5	1.5	2.7	2.0	2.7	2.1	–	–
Komba minor										
O	–	–	–	–	2.2	1.7	2.3	1.8	2.5	1.5
P	–	–	1.8	1.2	2.2	1.6	2.1	1.7	–	–
Q	–	–	–	–	–	*ca.* 1.8	2.2	1.8	2.6	1.5

thus yields some information on the anterior dentition not obtainable from other known specimens. Clark and Thomas (1952, pp. 5–6) concluded that C, the lateral incisiform tooth, was not fully taken over into the incisor series and that the three incisiform teeth were not as procumbent as in modern galagos. These characters are exceedingly difficult to judge from so imperfect a specimen. Comparison of broken alveoli with intact Recent jaws is especially confusing because roots and crowns are at a marked angle to each other and the alveoli give a false impression of the degree of procumbency of the crowns. After prolonged comparison, I cannot confirm the reality of any definite morphological distinction between this fossil and the corresponding parts of Recent *Galago*. Certainly the peculiar specialization of the anterior teeth in Recent lorisids was at least nearly and probably quite attained already in the Miocene.

KOMBA[1] new genus

Type-species: *Komba robustus* (Clark and Thomas, 1952).

Known distribution: Miocene of Kenya; Songhor, Rusinga, and Koru.

Diagnosis: Lorisids with dental formula and general aspect of dentition as in the Recent genera. Similar to *Progalago*, but differing as follows: P_4 with talonid narrower relative to trigonid, main cusp more medial or posterior, more distinct cuspule (metaconid?) posterolingual to main cusp; cusps of molars more acrodont; molar trigonids higher than talonids; trigonids rela-

[1] Komba is the Kiswahili name for species of *Galago*. Gender in the Latin sense does not occur in Kiswahili. The generic name is arbitrarily taken as masculine.

tively large, subtriangular, with anterobuccal cuspule; mandible shallow under M_3.

Discussion: Clark and Thomas distinguished their species "*Progalago*" *robustus* and "*P.*" *minor* primarily by size, but also mentioned for both the shallower mandible. As noted in the foregoing diagnosis, these two species share other well-marked morphological differences from typical *Progalago*. The differences seem to me definitely greater than between, for instance, Recent *Galago* and *Euoticus*, and on that basis they are ranked as generic. The two species are sharply distinct and it is even possible that if better known they would have to be placed in two genera.

Komba robustus (Clark and Thomas)

Progalago robustus Clark and Thomas, 1952, p. 9.

Holotype: Specimen H of consolidated list.

Hypodigm: Specimens H, I, J, K, and L. Specimens M and N are doubtfully referred and not included in the hypodigm. Reference of parts of skulls (specimens AB, AC, and AD) is still more dubious.

Known distribution: Miocene; Songhor and R3a and Gumba on Rusinga. Doubtfully Koru and R2 on Rusinga.

Diagnosis: Markedly larger than *K. minor*. Measurements of lower teeth as in Table 3. No cingula on lower molars.

Discussion: The diagnoses here given for *K. robustus* and *K. minor* are the same as those by Clark and Thomas so far as comparison of just these two species is concerned. Except specimen K, which adds nothing of interest, the specimens in the hypodigm of *robustus* were adequately described by Clark and Thomas. Doubtfully referred specimens M and N were not known to them.

Specimen M has each dimension of M_{2-3} within the probable size range of *K. robustus*, but these teeth are narrower relative to their length than in specimens more surely referable to that species and the trigonids seem also to be slightly larger in relative area.

Specimen N is of special interest as the only lorisid lower jaw from Koru. It so nearly resembles the type of *K. robustus* that it is perhaps straining at a gnat not to refer it to that species, or even to include it in the hypodigm. Yet the teeth do have a somewhat more slender but squatter (lower-crowned) look, and the trigonids of M_{1-2} are somewhat more distinctly triangular. The two localities may be slightly different in facies, at least, and although the identification is probable, I cannot consider it quite certain.

Komba minor (Clark and Thomas)

Progalago minor Clark and Thomas, 1952, p. 11.

Holotype: Specimen O of consolidated list.

Hypodigm: Specimens O, P, and Q.

Known distribution: Miocene of Songhor and Rusinga site R1a.

Diagnosis: Smaller than *K. robustus* and with small external cingula on the molar trigonids and between protoconids and hypoconids.

Discussion: The well-preserved molars of the type were correctly described and figured by Clark and Thomas. Specimen P, unknown to them, adds knowledge of P_4. This is structurally like the type of *K. robustus* but relatively shorter and wider with reduced talonid. Even in those characters of proportion it is closely similar to P_4 of specimen I, which is referred to *K. robustus* with reasonable confidence.

PROPOTTO[1] new genus

Type-species: *Propotto leakeyi* new species.

Known distribution: Miocene of Kenya: Songhor and probably Rusinga.

Diagnosis: Lorisids with variable lower cheek teeth closely resembling those of *Perodicticus*. P_3–M_3 rounded, ovate in out-

[1] Meant to imply an antecedent but not necessarily ancestral relative of the potto. Although the valid generic name of the potto is probably *Perodicticus*, *Potto* has also been used. The valid specific name of the potto is probably *Perodicticus potto* although several other names are also in use.

TABLE 4. MEASUREMENTS IN MILLIMETERS OF LOWER TEETH OF *Propotto leakeyi* FROM KENYA. Methods and conventions as in Table 3.

Specimen	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
R	3.3	2.1	3.3	2.5	3.9	3.1	3.8	3.2	–	–
S	–	–	3.5	2.3	4.0	3.5	–	–	2.7	2.1
T	–	–	–	–	–	–	3.6	2.9	3.3	2.3

line with low, blunt, poorly defined cusps. P_4 not oblique, excavated anterointernally and with vague metaconid; talonid with shallow basin, papillated. M_{1-2} with low, blunt, almost median protoconid and smaller metaconid posterointernal to it. Talonids basined, with blunt hypoconid; entoconid region papillated without clear definition of cusps. M_3 reduced, essentially a flattish crown with a central basin surrounded by a vaguely cuspidate rim.

Discussion: The apparently degenerate characters of the highly peculiar cheek teeth of this genus are like those in the Recent *Perodicticus* but may be even more extreme in the fossils. The details are so extremely variable in both that it is conceivable that almost any apparently diagnostic feature of the fossils might recur in the living forms, but in fact I cannot match all the characters listed above in a fair series of *Perodicticus* jaws and generic distinction seems warranted. Another possible distinction is that all three of the fossil jaws seem to deepen forward in a peculiar way that I have not seen in *Perodicticus* but that is approached in some specimens of its Asiatic vicar *Nycticebus.*

The three specimens on which this genus is based were not known to Clark and Thomas, and they have not heretofore been mentioned in print.

Propotto leakeyi[1] new species

Holotype: Specimen R of consolidated list.

Hypodigm: Specimens R, S, and T.

[1] Named for Dr. L. S. B. Leakey, in gratitude and admiration.

Known distribution: Miocene, Songhor, and probably Rusinga.

Diagnosis: Only known species of the genus. Measurements of lower teeth as in Table 4.

Discussion: The generic diagnosis calls attention to the most striking features of these specimens, and the accompanying figures obviate need for further verbal description. These peculiar dentitions are unlike any previously described in fossils and resemble those of the living pottos but are perhaps even more extreme in modification of the more primitive, more insectivore-like cheek teeth of other lorisids. The three specimens vary markedly in size, proportions, and structure of the teeth and at first sight seem hardly compatible with reference to a single species. However, *Perodicticus potto* is almost if not quite as variable in the same ways, and valid separation of species among the fossils will require larger samples, if it is called for at all.

SKULLS AND UPPER DENTITIONS

No associated upper and lower dentitions are known. The one Uganda specimen, the facial part of a skull, is the only nomenclatural type including upper teeth. As it cannot be compared with the Kenya types, it is a special case.

The Kenya specimens of skulls and upper teeth are from the same localities or areas as the lower jaws, including the five nomenclatural types, and it is presumable that they may for the most part if not altogether represent the same species. As is almost always true of fossil mammals, more lower than upper teeth and jaws are known.

Lower teeth of *Progalago dorae*, *P. songhorensis*, *Komba robustus*, and *K. minor* fall into four corresponding size groups without overlap among the known samples. *Propotto leakeyi* is of about the same size as *Progalago dorae*, but it is so distinctive morphologically that its upper teeth could almost surely be recognized if found. (They are not known.) The smallest species known from lower dentitions, *Komba minor*, should be recognizable by its size, or, at least, upper teeth too large to occlude can be excluded from consideration. In fact none of the upper teeth here available could belong to this species.

There remain three species of different sizes based on lower jaws and teeth: *Progalago dorae*, *P. songhorensis*, and *Komba robustus*, in sequence of decreasing size. Of the eight specimens with upper teeth, one (AI of consolidated list) is so poorly preserved as not to warrant any attempt at identification. The other seven do fall into three groups as regards size. They are here taken as possibly corresponding with the three named species based on lower jaws. These references are, however, quite uncertain. The skull and upper tooth specimens are not included in specific hypodigms (except *Miocuoticus bishopi*) or definitely referred to species. They are here described as cf. *Progalago dorae*, etc.

MIOEUOTICUS[1] Leakey

Type-species: *Mioeuoticus bishopi* Leakey.

Mioeuoticus Leakey, in Bishop, 1962, p. 6.

Known distribution: Miocene, Napak, Uganda.

Diagnosis: P^2 elongate; two-rooted. P^3 also elongate; three-rooted. P^4 ovoid; two main cusps; not molariform. M^{1-2} subquadrate; corners rounded; not emarginate posteriorly; less transverse than in most Recent galagines (but cf. lorisines); hypocone large, almost directly posterior to protocone; external cingulum present but narrow. M^3 ovoid; relatively large; tricuspid. Depth of anterior zygomatic root about as in *Galago* (less than in *Perodicticus*, more than in *Euoticus*).

Discussion: In his original generic diagnosis Leakey noted resemblances to the form here called cf. *Progalago dorae* but said that the "upper molars differ markedly . . . in lacking the very well-defined cingulum." The molars are worn and not perfectly preserved, which has somewhat obscured the cingulum, but study under high magnification shows that M^{1-3} do have external and partial posterior cingula. These are weaker than in cf. *Progalago dorae* but stronger than in cf. *Progalago songhorensis*. In further description of the type, Leakey stated that the palate is much shallower than in what I call cf. *Progalago dorae*, that "the arrangement of the teeth in the palate" (not otherwise specified or described) is like *Euoticus* and not *Galago* or cf. *Progalago dorae*, and that the root of the canine was set differently (the difference not specified) from cf. *P. dorae*, *Galago*, or *Euoticus* and more as in *Perodicticus*. The palate of the Napak specimen is crushed and I do not believe that anything really distinctive about its degree of shallowness can be surely established. These characters must be quite variable and nondistinctive in Recent galagines, for the specimens seen by me do not clearly agree with Leakey's statements about those used by him for comparisons. The point about arrangement of the teeth in the palate may refer to an apparently greater canting inward of the molars in *Euoticus* than *Galago* or cf. *Progalago dorae*, but in this respect *Miocuoticus* seems to me more like the latter two forms than like *Euoticus*. This, too, is affected by crushing and not reliable. I do not see any clear and constant difference in the way the canines are set in the groups mentioned.

In short, I do not see any likely generic distinctions between the type of *Miocuoticus bishopi* and specimens tentatively referred

[1] *Mioeuoticus* in the original publication. The hyphen must be deleted under the International Code of Zoological Nomenclature Article 32(c)(ii).

TABLE 5. MEASUREMENTS IN MILLIMETERS OF UPPER TEETH OF MIOCENE LORISIDAE FROM KENYA
Methods and conventions as in Tables 3–4.

	P^4		M^1		M^2		M^3		M^2
	L	W	L	W	L	W	L	W	L/W
cf. *Progalago dorae*									
AA	3.0	3.4	3.9	4.6	4.1	5.5	3.8	4.8	1.34
cf. *Komba robustus*									
AB	2.3	2.7	2.9	3.7	2.8	3.8	–	–	1.36
AC	–	–	–	–	2.9	4.2	2.6	3.9	1.45
cf. *Progalago songhorensis*									
AE	–	–	3.5	4.1	3.4	4.2	2.8	4.0	1.24
AG	–	–	–	–	3.7	4.6	–	–	1.24
AH	3.0	3.1	*ca.* 3½	–	3.5	–	–	–	
Mioeuoticus bishopi									
AJ	2.2	3.1	3.5	4.0	3.2	4.1	2.9	3.8	1.28

	P^2		P^3	
	L	W	L	W
cf. *P. dorae*				
AF	3.3	1.6	2.8	1.8

to *Progalago*, and I do not find it possible to frame a sound, differential generic diagnosis of *Mioeuoticus*. If the genus had not already been proposed, I would not propose it now. However, the reference of comparable specimens to *Progalago* is uncertain, *M. bishopi* is probably a valid species (if not genus), and it is not possible to establish a present probability that *Mioeuoticus* is *not* valid. I therefore do not formally reduce it to synonymy, pending hoped discovery of materials that might settle the question.

I am also unable to confirm that there is any special relationship between *Mioeuoticus* and *Euoticus*, especially as this is related to a similar supposed special relationship of cf. *Progalago dorae* to *Galago*. *Mioeuoticus* and *Progalago* are so closely similar and doubtfully separate that different relationships to Recent genera (although hypothetically possible) are not indicated by the specimens in hand. As Leakey did also indicate, *Mioeuoticus* (and I would add also *Progalago*) has quite eclectic resemblances to different Recent genera. P^4 is quite similar to that of *Perodicticus*, as Leakey noted, and also to *Arctocebus*. The proportions and outlines of the molars are also rather close to *Arctocebus*. The palate, orbital floor, and zygomatic root, however, are definitely closer to *Galago*, and so are the hypocones of M^{1-2}. The dental structure is on the whole less like *Euoticus* than like *Galago* or *Arctocebus*. P^2, not well preserved, is probably nearest to *Galago*.

Mioeuoticus bishopi Leakey

M. bishopi Leakey, in Bishop, 1962, p. 7.

Holotype: Specimen AJ of consolidated list.

Hypodigm: Type only.

Known distribution: Miocene, Napak, Uganda.

Diagnosis: Upper cheek teeth similar to cf. *Progalago dorae* but smaller, molars less transverse, cingula narrower. Size and proportions near cf. *Progalago songhorensis*, but corners somewhat more rounded and less suggestion of emargination on posterior border. Measurements as in Table 5.

Discussion: It is possible that this is the same species as cf. *Progalago songhorensis*, but that is not probable and the specimens are inadequate for a positive conclusion.

Cf. *Progalago dorae*

Specimens AA and AF of the consolidated list are appropriate in size and structure to occlude with lower dentitions of *P. dorae* and AA does in fact occlude well on actual trial, even though the specimens are certainly from different individuals. This generic and specific reference is thus reasonably probable although it cannot be certain.

AA, a nearly complete skull and much the best known fossil lorisoid, was described at length and well figured by Le Gros Clark (1956). Repetition of the description is unnecessary, but some supplementary remarks may be made.

The facial part of the skull is relatively larger, both in breadth and in depth, than in Recent lorisids of comparable over-all size. This is reflected not only in the very large, especially wide, palate but also in the broad interorbital region and the deep orbits. The orbital floor is low, broad, and comparatively flat, more or less as in *Euoticus* and small species of *Galago* and less like *Perodicticus*. The anterior root of the zygoma is correspondingly low and slender. In keeping with the depth of the skull, the anterior orbital rim, between the orbit proper and a shallow preorbital fossa on the face, is relatively long and more nearly vertical than in Recent lorisids.

In this family (and indeed in most mammals) a nuchal crest is largely a function of size and age, slight or absent in small species and young individuals, developed in old individuals of large species, including not only *Galago crassicaudatus* as noted by Le Gros Clark but also *Perodicticus potto* and *Nycticebus coucang*. This crest is, however, slightly stronger in the fossil than in any Recent specimen seen by me. Except for that slight difference and for the generally less swollen or globular braincase, the cranium of the fossil closely resembles that of *Perodicticus* in almost all respects.

A postorbital bar was almost certainly present and its upper root may have been about as in *Galago*, *Euoticus*, or *Arctocebus*, probably not as stout or as vertical as in the other three lorisines. There are two temporal ridges and they are most nearly like those of *Perodicticus*, although specimens of the small species of *Galago* (not *Euoticus*, which has a single ridge) are also similar.

The tympanic bulla is complete but is relatively smaller and less inflated than in any Recent lorisid, most nearly resembling *Nycticebus* as Le Gros Clark noted, but the difference from *Perodicticus* is slight. The auditory opening is circular and very large; there is no tendency to form a bony meatus. The mastoid inflation is relatively slight, but is not very different from *Perodicticus*.

Characteristic features of the dentition, noted by Le Gros Clark or evident in his figures, include: simple, nonmolariform P^4; subquadrate M^{1-2} with large hypocones posterior to protocones, relatively little transverse, with strong cingula, no posterior emargination; large, tricuspid M^3. The alveoli or roots indicate that the root of the lateral incisor was slightly larger than that of the medial incisor, that P^2 was two-rooted and elongated, that P^3 was three-rooted and also elongated, and that there are short diastemata between the roots of C and P^2 and P^2 and P^3—features unlike any Recent lorisid.

Specimen AF, described and figured by Le Gros Clark and Thomas (1952, pp. 7–8, pl. 3, fig. 9) probably belongs to the same species as AA (which was described later), and it confirms the preceding characters of the antemolar dentition except that it has no diastema between P^2 and P^3. Those two teeth are closely similar to *Galago crassicaudatus* and markedly unlike the shorter, more transverse teeth of all Recent lorisines.

Cf. *Progalago songhorensis*

Specimens AE, AG, and AH of the consolidated list are included here. They were unknown to Le Gros Clark and Thomas. They are fairly similar in morphology and

of about the same size, which is approximately that of *Progalago songhorensis*. It is, however, uncertain that they belong to a single species or that the species is *P. songhorensis*. AE, the best of the three specimens, is one of the two specimens of lorisids from Koru. It is, however, improbable that the species is the same as the other specimen (N) from Koru, a partial lower jaw with teeth too small to occlude with AE and probably outside the specific range.

The M^{1-3} of specimen AE differ from those of cf. *Progalago dorae* (specimen AA) not only in being smaller (Table 5) but also in being more transverse, less quadrate but with more sharply angular antero- and posteroexternal corners, anterior margin straighter and posterior margin slightly concave, hypocone of M^2, at least, less prominent, and cingula virtually absent. These differences are as great as between distinct genera of Recent lorisids, and AA and AE should perhaps be separated generically. It is doubtful, however, whether or not they represent previously named species, and proposal of another genus primarily on upper teeth seems undesirable for the present.

Comparable parts of molars of AG and AH differ somewhat from AE in size but have the distinctive characters noted above. AH includes P^4, which is very simple, bicuspid, with no clear indication of metacone or hypocone. It seems to be almost identical with P^4, less well preserved, in AA. Among Recent lorisids, it is near *Perodicticus* but is less rounded, with a more distinct parastylar projection, still more like *Nycticebus*. It is decidedly unlike any Recent galagine P^4.

Cf. *Komba robustus*

Specimens AB, AC, and AD of the consolidated list are placed here. Again it is uncertain whether these are really conspecific or whether the species is *K. robustus*, but they are not clearly separable specifically, they are from animals of about the same size, and the size is near that of *K. robustus*. Le Gros Clark and Thomas (1952) ascribed AC (M^{2-3}) to *Progalago dorae* and AD (cranium without teeth) to *Progalago* sp. at a time when all the Miocene lorisids were assigned to *Progalago* and there were no other upper teeth to compare with AC. Le Gros Clark later (1956) noted that AD is at least specifically and probably generically distinct from AA, referred by him to *Progalago* sp. and by me to cf. *Progalago dorae*. He also noted that M^{2-3} of AC are very different from AA. I agree, and to some extent that reinforces reference of these specimens to a genus judged distinct from *Progalago* on the basis of lower jaws and dentitions.

Specimen AB, with P^4–M^2, was not known to Le Gros Clark and Thomas. P^4 is basically bicuspid and, except for size and proportions, much like those referred to cf. *Progalago dorae* and cf. *P. songhorensis*. M^{1-2} are quite distinctive in outline, with strongly projecting metastylar lobes, strongly emarginate posterior border, and large hypocone decidedly posterolingual to the protocone. These characteristics are not exactly matched but are closely approached by *Galago alleni* (not other species of *Galago*) and *Loris tardigradus* among Recent lorisids. M^2 of specimen AC is almost like that of AB. M^3 is similar to M^2 but, as usual, with reduced metacone–metastyle and no hypocone. M^3 is relatively large.

AD, cranium with endocast partly exposed, was thoroughly described by Le Gros Clark and Thomas (1956, pp. 14–19, fig. 2,[1] pl. 1, and pl. 2, fig. 3). The individual represented is decidedly smaller than the skull cf. *Progalago dorae* (specimen AA), discovered later. The size difference is approximately that between lower jaws

[1] A drawing of the endocast. The cerebellar region is not exposed as the specimen is now preserved, and presumably the overlying bone was here removed to make the drawing and then replaced. Most of the bone removed from the skull roof for that purpose, as seen by a comparison of pl. 1 with fig. 2, of the text, was not replaced and is not now preserved with the specimen.

and dentitions of *Progalago dorae* and *Komba robustus*. The bullae of AD are relatively much larger and more inflated than those of AA and approach each other much more nearly on the basicranium. As Le Gros Clark and Thomas noted, they are about as large and inflated as in small species of *Galago*, and more so than in *Perodicticus* or *Nycticebus*. The porus is relatively smaller than in AA, probably less smoothly circular, and more as in Recent lorisids. As in AA, no long meatus is present.

RELATIONSHIPS

Although not large, the available collections include at least three genera and five species of lorisids of approximately the same age and from the same general region. It is by no means certain that all occurred together either at the same place or at the same time, but that would not be an ecological improbability. In Africa today there are at least four genera and seven species of lorisids with extensively overlapping ranges. Morphologically and, presumably, ecologically the fossils are almost as varied as the Recent forms. The four species now referred to *Progalago* and *Komba* are a rather compact group, probably somewhat less uniform than Recent Galaginae but not so diverse as Recent Lorisinae. *Propotto* is more aberrant in dentition, at least, and the difference from *Komba* is at least as great as between any two living lorisids.

The peculiarly specialized dentition of *Propotto* is definitely and uniquely similar to that of Recent *Perodicticus*. Parallelism cannot be excluded, but the most reasonable conclusion is that the two genera are closely and, among known forms, exclusively related. *Propotto* seems, if anything, to be rather more specialized than *Perodicticus*, but even direct ancestry of the genus *Propotto*, if not of the species *P. leakeyi*, to *Perodicticus* is possible.

The foregoing comparisons show that none of the other Miocene forms has clear and special resemblances to any one Recent genus, let alone species. Even among the few known parts, the resemblances are eclectic, each fossil resembling more than one different Recent species in different characters. The names *Progalago* and *Mioeuoticus* are misleading to the extent that they imply special resemblance or relationship. The fossils also have characters not precisely matched in any Recent species, but these are surprisingly minor and in no case striking. (If *Perodicticus* did not happen to survive, the peculiarities of *Propotto* would be very striking.)

If, as *Propotto* strongly suggests, a lineage generically allied to *Perodicticus* within the Lorisinae already existed in the Miocene, it would seem to follow that the Lorisinae and Galaginae were then differentiated. The difficulty of distinguishing those subfamilies by anatomical parts preserved in the fossils was mentioned in the preceding remarks on Recent lorisids. In the character most nearly diagnostic[1] of the subfamilies in those Recent forms, the structure of P_4^4, all the fossils are more like the Lorisinae. That might merely indicate that primitive, nonmolariform P_4^4 had not yet been lost in Miocene Galaginae. In other respects, all the fossils (except *Propotto*) have a mixture of resemblances to both Recent galagines and lorisines. It may be somewhat improbable, but not impossible, that only lorisines would occur in the Miocene collections when galagines probably originated in Africa and are more diverse and abundant than lorisines there now. I am quite uncertain as to whether *Progalago*, *Komba*, and the dubious genus *Mioeuoticus* are galagines, lorisines, or neither, and I must now classify them simply as Lorisidae, *sensu lato*. *Propotto* is doubtless a lorisine if the distinction is valid for the Miocene.

All the basic specializations of Recent Lorisidae are present in the known parts of the Miocene fossils. I do not detect any character in the fossils that is unquestionably

[1] Except for the pes, unknown in the fossils.

more primitive than in any Recent lorisid. Some Recent species are more specialized than the fossils in one way or another. For example, the mastoid inflation is greater in Recent galagines than in either of the two Miocene specimens revealing that character, but one of those specimens is more inflated than some Recent lorisines and the other is not much, if any, less inflated. The dental specialization of *Propotto* is at least as great as in any Recent lorisid. The molarization of P_4^4 is less in the fossils than in Recent Galaginae, but as great as in Recent Lorisinae. Over-all, the fossils provide no evidence of progressive change since the Miocene, which perhaps is not surprising in what has long been considered a primitive group as living primates go.

Nevertheless, the lorisids are not generalized mammals or generalized primates. They have distinct specializations, notably in dental formula and differentiation of antemolar teeth. The ectotympanic, annular but fixed in the lateral wall of the bulla, is unique among Recent primates. These specializations were present in the Miocene, and their rise should permit recognition of earlier relatives if specimens are found. Simons (1962) has pointed out that *Pronycticebus* and *Anchomomys* resemble lorisoids in several respects. Those are Eocene or (for *Pronycticebus*) early Oligocene European genera currently referred to the nominally lemuroid family Adapidae, *sensu lato*. The antemolar dentitions are poorly known and do not clearly have lorisoid specializations. Resemblances in P_4^4–M_3^3 are of a rather general nature, mostly in merely primitive characters and hardly more than, for example, in *Pseudoloris*, which despite its name is a tarsioid with no special relationships to lorisoids. Resemblances in skull proportions are also of a rather general and primitive or adaptive nature. Most suggestive is Simons' observation that the ectotympanic of *Pronycticebus*, although not definitely lorisoid, is in a condition that could be pre-lorisoid. A relationship is possible, but we are not justified in drawing a conclusion stronger than Simons' that, "Just possibly, these [loris-like features of *Pronycticebus*] can be interpreted as indicating the differentiation of the lorisiform prosimians from the general stock of the Adapidae (*s. l.*)." The Miocene lorisids do not really help to close the gap because in the known parts they are little if any more primitive than some, at least, of the Recent species.

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(Received 1 June, 1966.)

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Explanation of Plate 1

Figure 1. *Progalago dorae*. Type (specimen A of consolidated list), left mandibular ramus with P_4 and M_2. 1a, crown view. 1b, lingual view. Measurements in text.

Figure 2. *Progalago songhorensis*. Type (specimen E of consolidated list), left mandibular ramus with $M_{2\text{ a}}$. 2a, crown view. 2b, lingual view. Measurements in text.

Figure 3. *Komba robustus*. Type (specimen H of consolidated list), right mandibular ramus with P_3–M_2. 3a, crown view. 3b, lingual view. Measurements in text.

Figure 4. *Komba* cf. *robustus*. Specimen N of consolidated list, right mandibular ramus with P_4–M_2. Measurements in text.

Figure 5. *?Komba minor*. Type (specimen O of consolidated list), right mandibular ramus with $M_{1\text{ a}}$. 5a, crown view. 5b, lingual view. Measurements in text.

Figure 6. *Propotto leakeyi*. Type (specimen R of consolidated list), right mandibular ramus with P_3–M_2. 6a, crown view. 6b, lingual view. Measurements in text.

Figure 7. *Propotto* sp. Specimen S of consolidated list, left mandibular ramus with P_4–M_1 and M_3. Crown view. Measurements in text.

Figure 8. *Propotto leakeyi*. Specimen T of consolidated list, right mandibular ramus with $M_{2\text{ a}}$. Crown view. Measurements in text.

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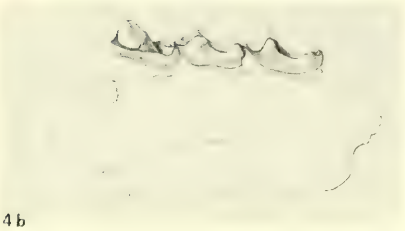
4a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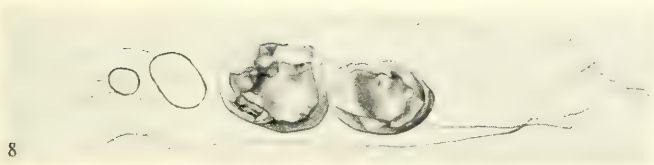
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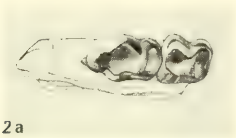
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7

5a

5b

Explanation of Plate 2

Figure 9. Cf. *Progalago dorae*. Specimen AA of consolidated list, right P^4–M^3. Crown view. Measurements in text.

Figure 10. Cf. *Progalago songhorensis*. Specimen AE of consolidated list, left M^{1-3}. Crown view. Measurements in text.

Figure 11. Cf. *Komba robustus*. Specimen AB of consolidated list, left P^4–M^2. Crown view. Measurements in text.

Figure 12. *Mioeuoticus bishopi*. Type (specimen AJ of consolidated list), left P^4–M^3. Crown view. Measurements in text.

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Bulletin OF THE
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The Ameghinos' Localities for Early Cenozoic Mammals in Patagonia

GEORGE GAYLORD SIMPSON

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 4
SEPTEMBER 29, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

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Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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THE AMEGHINOS' LOCALITIES FOR EARLY CENOZOIC MAMMALS IN PATAGONIA

GEORGE GAYLORD SIMPSON

INTRODUCTION

Early Cenozoic South American mammals, earlier than what was then called the *Pyrotherium* (now Deseadan) fauna, were discovered in Patagonia by Carlos Ameghino on his expedition of 1895–1896. They were first published by Carlos' elder, more articulate brother Florentino in 1897 (see Ameghino, 1897). It was not then recognized that the collections in hand included older forms, and at that time all were considered as from the "couches à *Pyrotherium*." On his expedition of 1898–1899, Carlos observed that there was included an older fauna, for which he suggested the name *Notostylops* fauna, and at the beginning of his following summer's work, 1899–1900, he noted that in fact there were two pre-*Pyrotherium* faunas. These observations were made to Florentino in letters from Carlos, 15 February 1899 and 9 October 1899, published much later in volume 21 of the "Obras completas" (Ameghino, 1913–1936). Florentino applied the name *Astraponotus* to the third fauna to be recognized, intermediate between the *Notostylops* and *Pyrotherium* faunas. The *Notostylops* fauna is now referred to the Casamayoran and the *Astraponotus* fauna to the Mustersan.

Carlos continued to collect from those early faunas into 1903, and he also was able to correct the allocation of specimens at first incorrectly ascribed to the *Pyrotherium* fauna. Florentino continued to publish brief descriptions of the specimens and to name a great number of new genera and species in the pre-*Pyrotherium* (pre-Deseadan) faunas through 1904. In 1906 he summarized them, with full generic faunal lists, in his great work on the mammal-bearing sedimentary formations of Patagonia (Ameghino, 1906). Some, but not all, of his published diagnoses were accompanied by a statement as to locality, but so generalized that the actual sites could hardly be relocated from these data alone. Almost all the specimens of the Ameghino Collection, now in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, have taxonomic labels in Florentino's hand on small slips of paper and some, but far from all of these, have locality data in the same vague terms as those used in publication. The 1906 volume has sketch maps by Carlos showing exposures and assumed connections of the "notostylopéen" (Casamayoran stage) and "astraponotéen" (Mustersan stage), but these are crude and likewise rather vague. (That is not an adverse criticism; there were no adequate maps of interior Patagonia in 1903 and earlier, and Carlos necessarily worked under extremely primitive and difficult conditions.) Copies of those maps are given in Figures 1 and 2 of the present paper.

It is essential for the interpretation of these faunas and for further discovery and study to locate Carlos Ameghino's localities

as well as possible. Partly to that end, I followed in his footsteps in Patagonia in 1930–1931 and 1933–1934 (principal localities in Fig. 3 of this paper), and I studied the Ameghino Collection and compared it with later collections of more precisely known provenience. Periodically since 1934 I have worked on the systematic augmentation and revision of the pre-Deseadan faunas. Part one was published long since (Simpson, 1948), and part two, completing the systematics, has now been finished and is in the editor's hands. Available locality data for many of the Ameghinos' specimens are there given in their terms. Further discussion of those localities, attempts to place them more precisely, and lists of type specimens from them are the subjects of the present paper.

The most important data for this study were derived from lengthy discussions with Carlos Ameghino in 1931. It was then 28 years since he had been in Patagonia, and these discussions occurred during a remission in a long, eventually fatal illness. His memory at that time cannot be considered infallible, but it was exceptionally clear. He had been accustomed to keep field notes in his head rather than on paper, and while this is extremely unfortunate from one point of view, it did have the advantage of making his unaided memory more reliable. Of course since he had been exploring in mostly unmapped territory, he could not have precise memory of locations not precisely determined at the time. Most of his statements agree with all other available information, but in just one instance (specified below) his memory was demonstrably at fault. I took written notes of these discussions, so the present report does not add failures of my memory to the record.

CASAMAYORAN LOCALITIES

Colhue-Huapi. That is the official spelling of the name of the larger, more eastern of the two major central Patagonian lakes. The name was used in this form by Florentino in publication. It does not, however, represent the local pronunciation, and the Ameghinos' specimen labels use variants that do represent local usage: Colhuapi, Coluapi, Colihuapi. This designates the great *barranca* (in Patagonia a cliff or scarp, not, as in some Spanish dialects, a ravine) south of the lake. It is not so distant from the lake or so extended north and south as suggested by Carlos' sketch map. In 1894–1895 Carlos had worked along a coastal area far to the southeast, including Punta Casamayor, now type locality for the Casamayor Formation and Casamayoran stage. However, at that time he did not find pre-Deseadan mammals there. He positively affirmed to me, and collection data and all other evidence are in accordance, that pre-Deseadan mammals were first found in 1895–1896 in this barranca. All the pre-Deseadan forms described in 1897 were from there. Both the "*Notostylops* fauna" and the "*Astraponotus* fauna," our Casamayoran and Mustersan faunas, were first found and (although later) recognized there, and a majority of all Ameghino specimens of both ages are from there. In fact the barranca has richly fossiliferous exposures of four stages in continuous sequence: Casamayoran, Mustersan, Deseadan, and Colhuehuapian, from bottom to top. It is the most imposing and important single known fossil mammal locality in South America, and one of the most important in the world. It must also be considered the greatest single discovery of Carlos Ameghino's extraordinary career. Among Ameghino's pre-Deseadan type specimens, 93 are labeled as from here, and according to Carlos most of the types not labeled as to locality are also from here.

A few specimens are indicated as from "Colhué-Huapí Sud." That is the same locality.

Oeste de Río Chico. The Río Chico is an intermittent stream carrying overflow from Lake Colhué-Huapí northeast to the Río Chubut. This designation by Carlos Ameghino refers to a long sequence of expo-

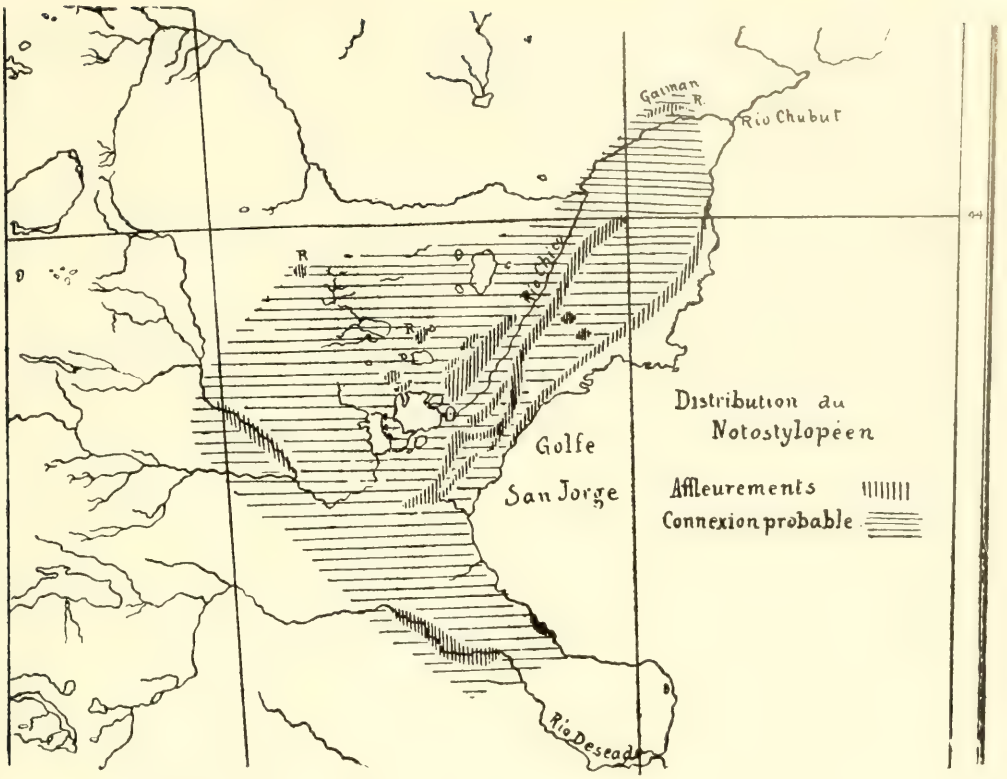

Fig. 1. Sketch map of central Patagonia with exposures and probable connections of the *Notostylops* beds (Casamayor Formation), by Carlos Ameghino. (From F. Ameghino, 1906, fig. 22.)

sures along the left, northwest bank of the Río Chico and on its small intermittent tributaries from the Pampa Pelada, along the upper third or half of the Río Chico valley between Lake Colhué-Huapí and the locality known to Carlos as Paso Niemann, called Puente Viejo or Puente Nollmann in the 1930's, and probably now called by still another name. (As in many sparsely inhabited areas, such as much of southwestern United States, map names in Patagonia are often unknown to the local inhabitants, and names used by them tend to change with each generation or oftener.)

Known fossil mammals from this region are all Casamayoran. Seventy-three Ameghino types are labeled as from this rather extensive area, and none can now be located more precisely. The rich pocket designated Cañadón Vaca in our field data, found by us in December, 1930, is in this area, and the assemblage more nearly resembles the Ameghinos' specimens from "Oeste de Río Chico" than those from "Colhué-Huapí." Nevertheless, Carlos was quite positive that he had not found our Cañadón Vaca pocket and that although his "Oeste de Río Chico" specimens were from near there, none were found precisely there.

Río Chico 1er yac. Pyroth. This abbreviated specimen label stands for "Río Chico, primer yacimiento de *Pyrotherium*," "Río Chico, first site or deposit of the *Pyrotherium* fauna," although in fact it was not the first known locality for that fauna (= Deseadan). On at least one poorly legible

label the indication seems to be rather "fr" than "1er" and could stand for "frente" (opposite). In either case, Carlos confirmed that this is the very rich Deseadan locality later also worked with great success by Loomis (1914a) and called Cabeza Blanca. Loomis, sharply and unjustifiably critical of the Ameghinos, insisted that there are no *Notostylops* or Casamayoran beds at this locality, although in fact he camped on those beds for three weeks. Carlos did collect Casamayoran fossils there, but only a few, including one type. We also found a few Casamayoran fossils there and in similar exposures extending for a league or more down the valley from the hill ("cabeza") itself, on the same side of the watercourse.

Río Chico. Three types have only this general label. Carlos could not place them more exactly.

Río Chico frente a Malaspina. Malaspina is an occupied site west of Bahía Bustamante, about half way between the coast and the Río Chico. The fossil locality is on the Río Chico, approximately at its nearest point to Malaspina. This is northeast (down the valley) from Cabeza Blanca and, as confirmed by Don Carlos, it was the northernmost point where he found Casamayoran mammals. Only one type and one other specimen are labeled as from here.

Colhuapi [*Colhué-Huapí*] *Norte.* This is an important locality, but it remains somewhat uncertain. Ameghino's sketch map (1906, fig. 22; Fig. 1 of this paper) shows two localities north of Lake Colhué-Huapí, one across the peninsula that juts into the north part of the lake, indicated as including "notostylopéen" and "pyrothéréen" (Casamayoran and Deseadan), and one northwest of that, shown as including "notostylopéen" and "astraponotéen" (Casamayoran and Mustersan). Thirteen Casamayoran and two Mustersan types in the Ameghino Collection are labeled "Colhuapi norte." We found exposures of both those stages and also Deseadan in this general area and an especially rich Mustersan deposit, with less common Casamayoran and Deseadan nearby, at a locality called (when we were there) Pajarito, on the west side of the Cerro del Humo. With allowance for the general inaccuracy of the Ameghino map and for its rotation of the lakes from their true orientation, our Pajarito could be precisely "Colhuapi norte," but Carlos emphatically denied this. He spoke of a single locality some distance from the lake on the slope of a meseta, probably in the vicinity of what was called the Sierra del Toro in the 1930's. The collections tend to support Don Carlos' opinion that the localities are not the same, ours being mostly Mustersan and his mostly Casamayoran (13 types, plus only 2 Mustersan). Also he found no Deseadan fossils there, and there are fairly evident fossiliferous Deseadan beds near our locality.

Santiago Roth, collecting for the La Plata Museum, found a rich Mustersan fauna at the locality that he called "Lago Musters" (see Simpson, 1936). This is almost certainly the same as our "Pajarito" or "Cerro del Humo," for our collection includes specimens of some of the same species preserved in the same way. By the same token, Roth's "Lago Musters" locality is probably not the Ameghinos' "Colhuapi norte." (Although the lake called "Musters" by Roth was in fact Colhué-Huapí and not the real Lago Musters.) The Ameghinos' maps do not show anything that could be Roth's "Lago Musters" locality, but do show a Casamayoran locality ascribed to Roth more to the north, perhaps near Cerro Talquino. There are in fact extensive mammal-bearing pre-Deseadan beds around Cerro Talquino, but I have been unable to equate these with any of Roth's highly inadequate site indications. Most of the information passed on by Roth to the Ameghinos was quite unreliable. Don Carlos' "Colhuapi norte" may possibly be Roth's "Lago Musters" and our "Pajarito" or "Cerro del Humo," but it is more likely that it has not been rediscovered. It is probably somewhat farther east than Carlos' sketch map indicates.

Pico Salamanca. This small peak is along

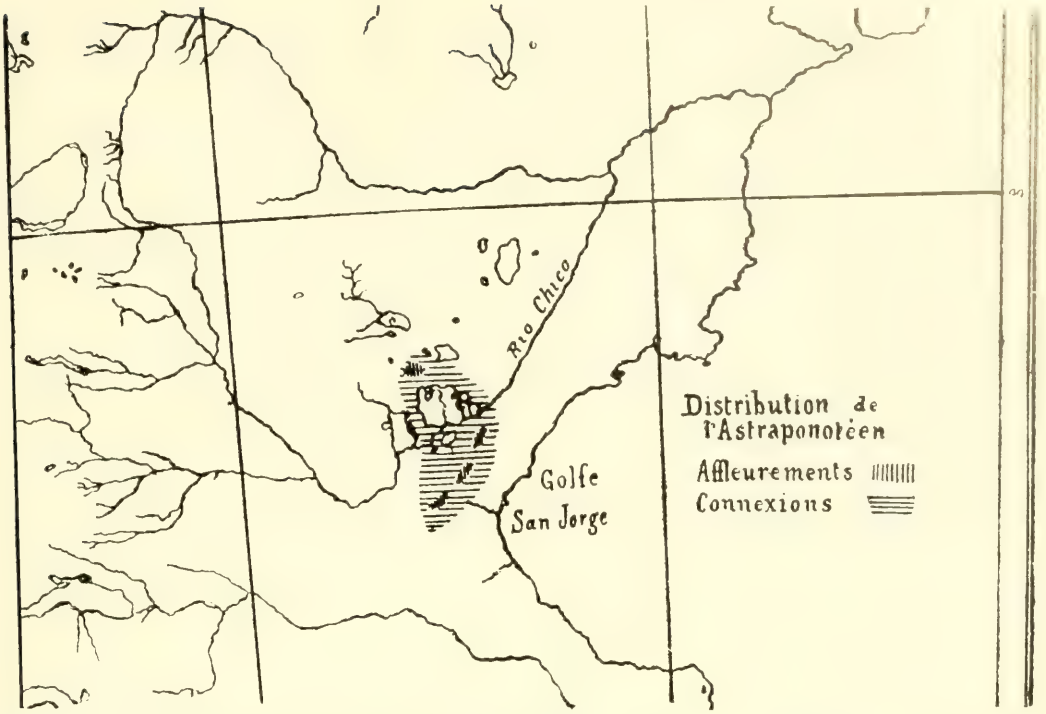

Fig. 2. Sketch map of central Patagonia with exposures and probable connections of the *Astraponotus* beds (Musters Formation), by Carlos Ameghino. (From F. Ameghino, 1906, fig. 23.)

the coast some 35 kilometers north of Comodoro Rivadavia. The peak itself includes no Casamayoran (nor Salamancan, although that stage is named for it), but it is surrounded by Casamayoran. Don Carlos said that fossils so labeled were gleaned over a large area in this general region. They include three types. Carlos' sketch map shows a long stretch of Casamayoran exposures roughly parallel to the coast, along the southeast flank of the Pampa de Castillo and the Meseta de Montemayor, approximately from Pico Salamanca to Punta Lobos. The formation does have about this extent, but the exposures are not as continuous as indicated.

Este de Río Chico. Don Carlos stated that this indication does not refer to the Río Chico valley but to the east slope of the Pampa de Castillo between the area called "Pico Salamanca" to the south and that called "Malaspina" to the north. One type (*Thomashuxleya externa*) is so labeled.

Malaspina. By this name Don Carlos indicated the area below, east, of Malaspina, around our locality "Las Violetas." He found only scraps here, and while we considered some of the exposures probably Casamayoran we found no fossils in them.

Casamayor. Punta Casamayor is in Santa Cruz, on the coast of the Gulf of San Jorge, roughly halfway from Comodoro Rivadavia to Cabo Blanco. Casamayoran exposures occur, not at Punta Casamayor but southeast of there along the coast between that point and Puerto Mazaredo and especially in a small *cañadón* that the Ameghinos named after the French collector Tournouër, whom they guided to this spot. That name was never known locally and in the 1930's, at least, the cañadón was known as "Lobo" (meaning "seal," not "wolf"). Tournouër

found a few fossils there, but more at Colhué-Huapí. Dealing with those fossils, Gaudry applied the name Casamayor to the formation now known by that name, which in turn has given its name to the Casamayoran stage and age. (On the Tournouër Collection and Gaudry's studies see Simpson, 1965.)

It has generally been assumed that Casamayor is a major locality for Casamayoran fossils, but such is not the case. The Ameghino Collection contains only one, unidentified specimen labeled as from there. Tournouër, most successful, found about a dozen identifiable specimens (described in Simpson, 1965). Loomis found only unidentifiable scraps (Loomis, 1914b), and Riggs and, later, I found just enough to confirm the presence of Casamayoran (Simpson, 1948, and in press). Even Don Carlos was confused on this one point, for he insisted that this is a rich site. When I pointed out that his collections contain only one poor specimen labeled as from there, he indicated another as also from there, but in fact that was neither from Casamayor nor collected by him. (This was the only out-and-out error in his discussions with me.) Don Carlos added that the richest level is exposed only at low tide on the wave-cut bench ("*restinga*"), but in fact the whole thickness of the type Casamayoran Formation is exposed, and practically barren of fossils, along the shore. The only identifiable fossils positively known to come from that area are from somewhat inland, in Cañadón "Tournouër" or Lobo.

Other supposed localities. Carlos' sketch map (Fig. 1 here) shows two other large areas of outcrops as "notostylopéen" or Casamayoran, but he told me that these had been identified on stratigraphic grounds only and that he had never found identifiable fossils in them. There are no specimens so labeled in the Ameghino Collection or specified in Florentino's publications. To my knowledge, there is likewise no trustworthy later report of identifiable pre-Deseadan mammals in either place. One is on the Río Deseado between Pico Truncado and Jaramillo, and the other on the Río Senguerr west of the central lakes and of the Sierra San Bernardo.

Von Huene (1929, p. 16) wrote that, "A 50 o más kilómetros de aquí [western part of the Sierra San Bernardo], hacia el norte, se encuentran los lugares de hallazgos de los bellos y completos cráneos de *Notostylops*, que se encontraron depositados en tobas cenicientas, rojizas y claras, según me ha explicado personalmente don Carlos Ameghino al mostrarme esos cráneos. . . ." Some failure of communication had occurred. There is no known Casamayoran in the region indicated, none is shown on Don Carlos' sketch map, no specimens of *Notostylops* or anything else in the Ameghino Collection could be supposed to have that origin, and Don Carlos assured me that he had not made any such statement to von Huene.

MUSTERSAN LOCALITIES

Colhué-Huapí. Localities were given for extremely few of the Ameghinos' Mustersan ("astraponotéen") fossils. Three, all types, are labeled as from "Colhuapi," the same as for Casamayoran specimens from the barranca south of Lake Colhué-Huapí. Don Carlos confirmed that almost all his Mustersan specimens were from there. The sketch map for the "astraponotéen" shows three relatively small patches of exposures, all in the line that rather inaccurately indicates that barranca on the "notostylopéen" sketch map (compare Figs. 1 and 2 of this paper). The southwestern patch, evidently somewhat misplaced, may represent the western extension of the barranca known in the 1930's as Cerro Blanco, where we also found Mustersan fossils allied to "*Asmodeus*" *circunflexus*, now doubtfully referred to *Periphragnis*, the type of which is from Colhué-Huapí. (There is, however, some possibility that the type had drifted from the overlying Deseadan and represents one of the Ameghinos' extremely few errors of age determination.)

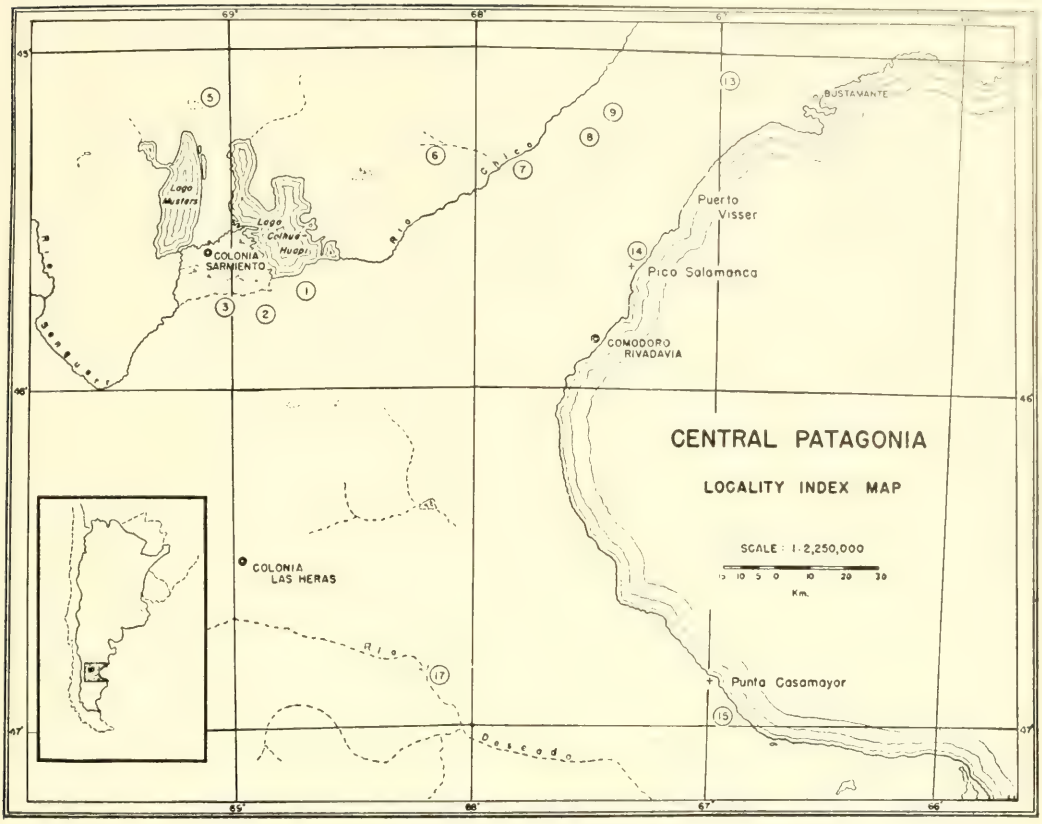

Fig. 3. Index map of central Patagonia, showing collecting localities of the American Museum expeditions (1930–1931, 1933–1934) relevant to Carlos Ameghino's earlier sites. 1, Barranca south of Lake Colhué-Huapí. 2, Kilometer 170, section similar to 1. 3, Cerro Blanco, essentially a westward extension of 1. 5, Pajarito or Cerro del Humo. 6, Cañadón Vaca, one of a series of Casamayoran localities west of the Río Chico. 7, Cañadón Hondo, one of a series of Casamayoran (and Riochican) localities east of the Río Chico. 8. Cabeza Blanca. 9, Site east of the Río Chico down the valley from Cabeza Blanca. 13, Las Violetas, in the region of Carlos Ameghino's "Malaspina." 14, Pico Salamanca. 15, Cañadón Lobo ("Cañadón Tournouër"). 17, Pico Truncado. (Slightly modified from Simpson, 1948, fig. 1.)

Colhuapi norte. This is the only other Mustersan locality on Don Carlos' sketch maps or on the specimen labels. It is the same as a Casamayoran locality and its dubious location has been discussed above.

SUBDIVISION OF CASAMAYORAN AND POSSIBLE REFERENCES TO RIOCHICAN

Florentino Ameghino at one time (1902) gave generic lists supposedly distinctive of a "Notostylopense superior" and "inferior," but later (1906), while still considering that three or perhaps four successive faunas occur, he united these into one "grande faune." A few specimens, mostly from Colhué-Huapí, were designated in publication or on labels as from the upper or the lower "notostylopense" or "notostylopéen." However, these do not suffice to distinguish separable faunas. In general, Don Carlos did not attempt to separate fossils of one "grande faune" by levels; when he collected, the desirability of such minor subdivision was not evident and with his facilities (or lack of them) its practicability was

slight. In fact, even though recent collections are exactly placed in stratigraphic sections and it seems highly probable that known Casamayoran covers an appreciable span, no distinct faunal succession has yet been established (e.g., Pascual, 1965).

F. Ameghino also referred to a "basal" "Notostylopense" or "Notostylopéen," without making it quite clear what sediments were meant to be included. He further stated that the Salamancan is limited (at its upper boundary) by "un ruban de grès à gros grains mélangés . . . avec des os . . . de Mammifères de la faune du *Notostylops*." He added that, "Une des plus intéressantes localités de ce ruban, est celle découverte par M. Roth en face de Gaiman . . . avec des dents et des ossements de Mammifères de la faune notostylopéenne, tels que *Notostylops*, *Polydolops*, *Didolodus*, *Adpithecus*, *Trigonostylops*, etc." (Ameghino, 1906, pp. 94–95). He was thus definitely including in the "notostylopéen" and perhaps, but not explicitly, as "basal" the beds that I much later (Simpson, 1933) called the Río Chico Formation. Most of the information, here and elsewhere, cited by F. Ameghino as coming from Roth was incorrect, perhaps even willfully so, as Roth and the Ameghinos were not invariably on good terms. It is true that Roth found a few mammals in sandstones near Gaiman, a settlement on the Chubut River, but the cited genera were not found, even according to Roth's identifications. Roth (1908) reported none of the genera named by Ameghino but two supposedly new genera, one perhaps synonymous with *Henricosbornia* (including "*Polystylops*") and one with *Isotemnus*. Roth did also have a specimen perhaps belonging to *Polydolops*, but none of the other genera reported by Ameghino (see Simpson, 1935a, b).

F. Ameghino's statement seems to imply that he also had specimens of the *Notostylops* fauna from the sandstone that he considered a shore facies of the Salamancan and that this was part of his "notostylopéen," perhaps the "notostylopéen basal." In fact this seems to have been an error based either on a misunderstanding or a deliberate misstatement from Roth and not on observations by Carlos or specimens collected by him. The Río Chico Formation, which of course is to be distinguished from the Riochican stage and age, is composed of detrital clays, sandstones and conglomerate. The Casamayor Formation, likewise as distinct from the Casamayoran stage and age, is entirely composed of volcanic bentonites and tuffs. The difference in aspect is so complete and striking that it cannot possibly be missed by the most casual observer, let alone as keen an observer as Carlos Ameghino. He categorically assured me that all his specimens referred to the *Notostylops* fauna were from the volcanic beds and that he never found a mammalian fossil in any lower beds. There is no fossil mammal in the Ameghino Collection similar in aspect, in adhering matrix, or as far as definitely determinable in species to known fossils from the Río Chico Formation. Incidentally, although the extreme uppermost beds of the Río Chico do have some genera in common with the Casamayor, *Notostylops* is not among them as far as yet discovered.

Caroloameghinia mater and *C. tenue* were published as from the "basal" *Notostylops* beds. The type specimens now have no associated horizon or locality data. Definitely identifiable referred specimens of each species are from the Casamayor Formation, and the genus has not been found in the Río Chico Formation (see Simpson, 1948). The type of *Pantostylops typus* is also labeled as from the "Partie basale" of the *Notostylops* beds, but this is a synonym of *Henricosbornia lophodonta*, a rather common Casamayoran species. The Ameghinos' three type specimens here in question almost certainly were from the Casamayor, and the unique reference to them as not only "inferior" but "basal" evidently means only that they were near the bottom of the Casamayor tuffs, not that they were in the Río Chico beds. As noted in discussing the species (Simpson, 1948, p. 165), the type of *Othnielmarshia lacunifera* has a word on

the label that may be "cuarcito" (quartzite), which could apply to Río Chico sandstone rather than to coarse Casamayor tuff. However, we found the species abundant in definitely Casamayor beds in the general area of the type locality ("Oeste de Río Chico"), where, furthermore, we found no Río Chico exposures. This specimen, too, is almost certainly from the typical Casamayor tuffs.

Whatever concept Don Florentino may have intended by "notostilopense basal," it was not based on fossils from the Río Chico Formation, and his *Notostylops* fauna did not include any species of Riochican age.

Confusion on these points was later compounded by the application of the name "Pehuenche" by Argentine government geologists and others to the beds now called Río Chico, the type Pehuenche being in fact entirely distinct and much earlier in age. Cabrera (1936) shared that confusion and also concluded that the Riochiquense, a virtual synonym of Pehuenche in this mistaken sense, may be equivalent to "una buena parte del Notostilopense de Ameghino." Debate on that point is made superfluous by the facts that none of the Ameghinos' fossil localities were in the beds in question and that they had no valid evidence for referring them to the "Notostilopense." (Cabrera referred a number of fossils from the uppermost Río Chico to Casamayoran species, but those are what might be called negative identifications: the specimens were not specifically identifiable on available data and were referred to species from which they could not be certainly distinguished but without positive evidence of pertinence to those species.)

LOCALITY DATA OF TYPE SPECIMENS

The following list includes the names of all Ameghino's Casamayoran and Mustersan mammalian type specimens for which I have been able to find locality data. Listing is first by family and within families in alphabetical order of the names first applied by Florentino Ameghino. When appropriate, that is followed in parentheses by the name used by me (Simpson, 1948, and in press) for the taxon to which I now refer Ameghino's type, if that name is different from the one first attached to his type by Ameghino. Available locality indications are given by the following abbreviations:

C.H.—Colhué-Huapí.
C.H.N.—Colhué-Huapí norte.
E.R.C.—Este de Río Chico.
O.R.C.—Oeste de Río Chico.
P.S.—Pico Salamanca.
R.C.—Río Chico.
R.C.M.—Río Chico, frente a Malaspina.
R.C.P.—Río Chico, yacimiento de *Pyrotherium* (around Cabeza Blanca).

Faunas or levels are indicated as follows:

Ca.—Casamayoran.
Ca.S.—Upper Casamayoran.
Ca.I.—Lower Casamayoran.
Mu.—Mustersan.

It is known that types of all pre-Deseadan species described in 1897 were from Colhué-Huapí and they are listed as such even though not so labeled in the collection.

Names as first proposed by Ameghino that do not appear in this list were based on specimens for which I have no field data.

MARSUPIALIA

Didelphidae

Ideodelphis microscopicus. C.H., Ca.

Borhyaenidae

Arminiheringia auceta. C.H.N., Ca.
A. contigua (*A. cultrata*). C.H., Ca.
A. cultrata. C.H., Ca.
Dilestes dilobus (*Arminiheringia auceta*). C.H.N., Ca.
Nemolestes spalacotherinus. C.H.N., Ca.
Procladostictis erecta ("*P.*" *erecta*). C.H.N., Ca.
Pseudocladostictis determinabile. C.H., Ca.

?Caenolestidae

Progarzonia notostylopense. C.H., Ca.

Polydolopidae

Amphidolops serrifer (*Polydolops serra*). C.H., Ca.
Amphidolops serrula. C.H., Ca.
Pliodolops primulus (*Polydolops primulus*). C.H., Ca.
Polydolops crassus (*P. thomasi crassus*). C.H., Ca.
Polydolops fur (*P. thomasi thomasi*). C.H., Ca.
Polydolops serra. C.H., Ca.
Polydolops simplex (*P. thomasi thomasi*). C.H., Ca.
Polydolops thomasi. C.H., Ca.
Pseudolops princeps (*Polydolops princeps*). C.H., Ca.

EDENTATA

Dasypodidae

Anteutatus lenis (*Utaetus lenis*). ?C.H., Ca.S.
Coelutaetus cribellatus. R.C., Ca.
?*Machlydotherium sparsus* (*M. sparsum*). C.H., Ca.S.
Meteutatus percarinatus. C.H., Ca.S.
Orthutaetus clavatus (*Utaetus buccatus*). C.H., Ca.I.
Orthutaetus crenulatus (*Utaetus buccatus*). C.H., Ca.S.
Parutaetus chicoensis (*Utaetus buccatus*). C.H., Ca. [The specific name strongly suggests a Río Chico locality, but the label with the type has "Colhuapi."]
Parutaetus clusus (*Utaetus buccatus*). C.H., Ca.S.
Parutaetus signatus (*Utaetus buccatus*). C.H., Ca.S.
Posteutatus indemnis (*Utaetus buccatus*). C.H., Ca.S.
Posteutatus indentatus (*Utaetus buccatus*). C.H., Ca.S.
Posteutatus scabridus (*Utaetus buccatus*). C.H., Ca.S.
Prostegotherium astrifer. C.H., Ca.S.
Prostegotherium notostylopianum. C.H., Ca.S.
Pseudostegotherium chubutanum. C.H., Ca.S.
Utaetus argos (*U. buccatus*). R.C.M., Ca.
Utaetus buccatus. C.H., Ca.S.
Utaetus deustus. C.H., Ca.S.
Utaetus laxus. O.R.C., Ca.

CONDYLARTHRA

Didolodontidae

Didolodus colligatus (*D. multicuspis*). C.H., Ca.
Didolodus multicuspis. C.H., Ca.
Enneoconus parvidens. O.R.C., Ca.
Euprotogonia patagonica (*Ernestokokenia patagonica*). C.H.N., Ca.
Euprotogonia trigonalis (*Ernestokokenia trigonalis*). C.H.N., Ca.
Lambdaconus mamma (*Paulogervaisia mamma*). C.H., Ca.S.
Lambdaconus porcus (*Paulogervaisia porca*). C.H., Ca.S.
Lonchoconus lanceolatus (*Didolodus multicuspis*). C.H., Ca.
Nephacodus latigonus (*Didolodus latigonus*). O.R.C., Ca.
Paulogervaisia inusta. C.H., Ca.S.
Proectocion argentinus. C.H., Ca.
Proectocion precisus. C.H., Ca.
Prohyracotherium medialis (*Archaeohyracotherium mediale*). O.R.C., Ca.

LITOPTERNA

Macraucheniidae

Amilnedwardsia brevicula. O.R.C., Ca.
Anisolambda longidens (?*Victorlemoinea longidens*). O.R.C., Ca.
Ernestohaeckelia acutidens. O.R.C., Ca.
Rutimeyeria conulifera. C.H., Ca.
Victorlemoinea labyrinthica. O.R.C., Ca.
Victorlemoinea emarginata. O.R.C., Ca.

Proterotheriidae

Guilielmofloweria plicata. C.H., Ca.
Josepholeidya adunca. O.R.C., Ca.
Josepholeidya deculca. C.H., Ca.
Ricardolydekkeria praerupta. C.H., Ca.
Ricardolydekkeria profunda. C.H., Ca.

NOTOUNGULATA

Henricosborniidae

Henricosbornia alouatina (*H. lophodonta*). O.R.C., Ca.
Henricosbornia subconica (*H. lophodonta*). O.R.C., Ca.
Othnielmarshia lacunifera. O.R.C., Ca.
Pantostylops incompletus (*Henricosbornia lophodonta*). O.R.C., Ca.
Pantostylops minutus (*Peripantostylops minutus*). O.R.C., Ca.
Pantostylops typus (*Henricosbornia lophodonta*). O.R.C., Ca.
Polystylops amplus (*Henricosbornia lophodonta*). O.R.C., Ca.
Polystylops progrediens (*Henricosbornia lophodonta*). O.R.C., Ca.
Postpithecus curvicrista (*Othnielmarshia curvicrista*). O.R.C., Ca.
Postpithecus reflexus (*Othnielmarshia reflexa*). O.R.C., Ca.
Selenoconus agilis (*Peripantostylops minutus*). O.R.C., Ca.
Selenoconus centralis (*Henricosbornia lophodonta*). O.R.C., Ca.
Selenoconus senex (*Henricosbornia lophodonta*). O.R.C., Ca.

Notostylopidae

Acrostylops pungiunculus (*Homalostylops parvus*). C.H., Ca.
Catastylops deflexus (*Notostylops deflexus*). C.H., Ca.
Catastylops pendens (*Notostylops pendens*). O.R.C., Ca.
Entelostylops appressus (*Notostylops appressus*). R.C.P., Ca.
Entelostylops completus (*Notostylops murinus*). C.H., Ca.
Entelostylops incolumis (*Homalostylops parvus*). C.H., Ca.
Entelostylops tripartitus (*Notostylops murinus*). O.R.C., Ca.
Eostylops diversidens (*Notostylops diversidens*). C.H.N., Ca.
Homalostylops interlissus. C.H.N., Ca.
Homalostylops rigeo (*H. parvus*). C.H., Ca.
Isostylops fretus (*Notostylops murinus*). C.H., Ca.
Notostylops ampullaceus (*N. murinus*). C.H.N., Ca.
Notostylops aspectans (*N. murinus*). O.R.C., Ca.
Notostylops bicinctus. C.H., Ca.
Notostylops chicoensis. C.H., Ca. [Despite the specific name, the type is definitely labeled Colhué-Huapí.]
Notostylops murinus. C.H., Ca.
Notostylops parvus (*Homalostylops parvus*). C.H., Ca.
Notostylops promurinus (*N. murinus*). C.H., Ca.

Oldfieldthomasiidae

Acoelodus connectus (*Paginula parca*). O.R.C., Ca.
Acoelodus oppositus. C.H., Ca.
Acoelodus proclivus. C.H., Ca.S.
Antepithecus plexostephanos (*Maxschlosseria minima*). O.R.C., Ca.S.
Eochalicotherium minutum (*Maxschlosseria minuta*). O.R.C., Ca.
Eostylops obliquatus (*Maxschlosseria consumata*). C.H., Ca.
Isotemnus consumatus (*Maxschlosseria consumata*). O.R.C., Ca.
Isotemnus emundatus (*Maxschlosseria rusticula*). O.R.C., Ca.
Maxschlosseria anatona (*M. minima*). O.R.C., Ca.S.
Maxschlosseria praeterita. O.R.C., Ca.I.
Oldfieldthomasia anfractuosa. C.H.N., Ca.
Oldfieldthomasia cingulata (*O. debilitata*). C.H., Ca.
Oldfieldthomasia conifera (*O. debilitata*). C.H., Ca.
Oldfieldthomasia cuneata (*O. debilitata*). C.H., Ca.
Oldfieldthomasia furcata (*O. debilitata*). C.H., Ca.
Oldfieldthomasia marginalis (*Maxschlosseria rusticula*). O.R.C., Ca.
Oldfieldthomasia parvidens. C.H., Ca.
Oldfieldthomasia plicata (*O. debilitata*). C.H., Ca.
Oldfieldthomasia pulchella (*O. parvi-*

dens). C.H., Ca.
Oldfieldthomasia septa (*Maxschlosseria septa*). O.R.C., Ca.
Oldfieldthomasia transversa. C.H., Ca.
Paginula parca. O.R.C., Ca.
Pleurostylodon minimus (*Maxschlosseria minima*). O.R.C., Ca.
Ultrapithecus rusticulus (*Maxschlosseria rusticula*). O.R.C., Ca.
Ultrapithecus rutilans. C.H.., Ca.

Archaeopithecidae

Adpithecus plenus (*Archaeopithecus rogeri*). C.H., Ca.
Archaeopithecus alternans (*Acropithecus rigidus*). O.R.C., Ca.
Archaeopithecus rigidus (*Acropithecus rigidus*). O.R.C., Ca.
Archaeopithecus rogeri. C.H., Ca.
Notopithecus fossulatus (?*Archaeopithecus fossulatus*). C.H., Ca.

Interatheriidae

Adpithecus subtenuis (*Notopithecus adapinus*). C.H., Ca.I.
Antepithecus brachystephanus. C.H., Ca.
Antepithecus innexus (?*A. innexus*). C.H., Ca.
Antepithecus interrasus (*A. brachystephanus*). C.H., Ca.
Epipithecus confluens (*Notopithecus adapinus*). P.S., Ca.
Gonopithecus trigodontoides (*Notopithecus adapinus*). O.R.C., Ca.
Infrapithecus cinctus (*Antepithecus brachystephanus*). C.H., Ca.
Infrapithecus diversus (*Notopithecus adapinus*). C.H.N., Ca.
Notopithecus adapinus. C.H., Ca.
Transpithecus obtentus. C.H., Ca.

Archaeohyracidae

Eohyrax isotemnoides. C.H., Ca.
Eohyrax praerusticus. C.H., Ca.
Eohyrax rusticus. O.R.C., Ca.S.

Isotemnidae

Amphitemnus nucleatus (*Isotemnus primitivus*). C.H., Ca.
Amphitemnus transitorius (*Isotemnus primitivus*). C.H., Ca.
Anchistrum sulcosum (*Pleurostylodon modicus*). C.H., Ca.
Anisolambda latidens (*Isotemnus latidens*). C.H.N., Ca.
Asmodeus circunflexus (?*Periphragnis circunflexus*). C.H., Mu.
Coelostylops crassus (*Pleurostylodon similis*). O.R.C., Ca.
Dialophus recticrista (?*Pleurostylodon recticrista*). O.R.C., Ca.
Dialophus simus (*Pleurostylodon modicus*). P.S., Ca.
Dimerostephanus attritus (*Pleurostylodon modicus*). C.H., Ca.S.
Dimerostephanus colhuehuapensis (?*Isotemnus colhuehuapensis*). C.H., Ca.S.
Eochalicotherium crassidens (*Isotemnus latidens*). O.R.C., Ca.
Eochalicotherium robustum (*Isotemnus latidens*). O.R.C., Ca.
Isotemnus apicatus (*I. latidens*). O.R.C., Ca.
Isotemnus conspiquus (*I. primitivus*). C.H., Ca.
Isotemnus distentus (*Anisotemnus distentus*). P.S., Ca.S.
Isotemnus enecatus (*I. latidens*). O.R.C., Ca.
Isotemnus lophiodontoides (*Anisotemnus distentus*). O.R.C., Ca.
Isotemnus primitivus. C.H., Ca.
Paratemnus geminatus (*Pleurostylodon modicus*). C.H., Ca.
Pleurostylodon divisus (*P. modicus*). C.H., Ca.
Pleurostylodon obscurus (*P. modicus*). R.C., Ca.
Plexotemnus complicatissimus (*Acoclohyrax complicatissimus*). C.H., Ca.
Porotemnus crassiramis (?*Pleurostylodon crassiramis*). C.H., Ca.S.
Thomashuxleya externa. E.R.C., Ca.
Thomashuxleya robusta. C.H., Ca.
Trimerostephanus angustus (*Isotemnus primitivus*). C.H., Ca.
Trimerostephanus biconus (*Pleurostylo-*

don biconus). C.H., Ca.
Trimerostephanus sigma (*?Acoelohyrax sigma*). C.H.N., Mu.
Tychostylops marculus (*Pleurostylodon modicus*). C.H., Ca.
Tychostylops simus (*Pleurostylodon similis*). C.H., Ca.

Notohippidae

[No locality data for Ameghinos' specimens.]

Notoungulata *incertae sedis*

Carolodarwinia pyramidentata. C.H., Mu.
?Claenodon patagonicus ("*Claenodon*" *patagonicus*, not this genus). R.C.M., Ca.
Isotypotherium annulatum. P.S., Ca.S.
Lophiodonticulus patagonicus. O.R.C., Ca.S.
Lophiodonticulus retroversus. O.R.C., Ca.S.
Pleurostylops glebosus. O.R.C., Ca.
Tonostylops spissus. C.H., Ca.

ASTRAPOTHERIA

Astrapotheriidae

Astraponotus assymmetrus. C.H.N., Mu.

TRIGONOSTYLOPOIDEA

Trigonostylopidae

Albertogaudrya oxygona (*A. unica*). C.H., Ca.S.
Albertogaudrya regia (*A. unica*). C.H.N., Ca.S.
Albertogaudrya separata (*A. unica*). C.H., Ca.S.
Albertogaudrya tersa (*A. unica*). C.H., Ca.S.
Scabellia cyclogona (*Albertogaudrya unica*). C.H., Ca.
Scabellia laticincta (*Albertogaudrya unica*). C.H., Ca.
Trigonostylops columnifer (*T. wortmani*). C. H., Ca.
Trigonostylops coryphodontoides (*T. wortmani*). C.H., Ca.
?Trigonostylops duplex ("*T.*" *duplex*). C.H., Ca.
Trigonostylops eximius (*T. wortmani*). C.H., Ca.
Trigonostylops germinalis (*T. wortmani*). C.H., Ca.
Trigonostylops hemicyclus (*T. wortmani*). C. H., Ca.
Trigonostylops insumptus (*T. wortmani*). C.H., Ca.
Trigonostylops integer (*T. wortmani*). C.H., Ca.
Trigonostylops minimus (*T. wortmani*). C.H., Ca.
Trigonostylops scabellum (*T. wortmani*). O.R.C., Ca.
Trigonostylops secondarius (*T. wortmani*). C.H., Ca.
Trigonostylops subtrigonus (*T. wortmani*). R.C., Ca.
Trigonostylops trigonus (*T. wortmani*). C.H., Ca.
Trigonostylops wortmani. C.H., Ca.

PYROTHERIA

Pyrotheriidae

Carolozittelia eluta. Published as from the lower part of the *Pyrotherium* beds (Deseadan), "Oeste de Río Chico, cerca Chubut," but may be from the Casamayoran.
Carolozittelia tapiroides. O.R.C., Ca.
Promoeritherium australe. C.H., Mu.

Mammalia *incertae sedis*

Anagonia insulata. C.H., Ca.S.
Proplanodus adnepos. C.H., Ca.S.

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(*Received 1 June 1966.*)

Bulletin OF THE
Museum of
Comparative
Zoology

A Study of the Effects of Expatriation on the Gonads of Two Myctophid Fishes in the North Atlantic Ocean

WILLIAM T. O'DAY AND BASIL NAFPAKTITIS

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 5
SEPTEMBER 29, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
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Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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A STUDY OF THE EFFECTS OF EXPATRIATION ON THE GONADS OF TWO MYCTOPHID FISHES IN THE NORTH ATLANTIC OCEAN

WILLIAM T. O'DAY[1] AND BASIL NAFPAKTITIS[1]

INTRODUCTION

Nearly a hundred years ago it was assumed that species of deep-sea fishes must have an unlimited horizontal distribution because of the apparent uniformity in their sunless environment. Material and knowledge have been increasing rapidly ever since, and we now know that even congeneric species can be localized in particular regions or water masses. We also know that some widely spread species can not reproduce away from their generally restricted spawning areas. Concerning this latter phenomenon, Ekman (1953: 317) wrote, "In some cases where a species occurs in a region as a dwarfed variety or with very few individuals, it may nevertheless reproduce itself to a sufficient extent and thus have its home there. But in other instances it remains questionable whether the species is able to exist independently in the unfavourable region or whether it would not die out there if it were not continuously reinforced from the more favourable regions." Ekman named the unfavourable region the expatriation area. His insight provided a new viewpoint for subsequent studies in zoogeography. "With the ever increasing store of specimens of bathypelagic fishes," wrote Ebeling (1962: 1), "along with accumulated data on their distributions and environment, it is now possible to discuss their zoogeography profitably; that is, to investigate not only what species are present and where they are, but also why they are there and how they got there."

Lantern fishes, family Myctophidae, offer good material for a study of expatriation in general and, especially, of its effects in the gonads at the cellular level. Most of them live at depths between 200 and 1,000 meters. Precise determination of the vertical distribution is complicated by several factors, especially the following: (1) distinct developmental stages are found at different depths; (2) after metamorphosis the fishes undergo extensive diurnal vertical migrations; (3) vertical distribution in the same species can vary in different areas.

Spawning depth seems to be species-specific. Fertilized eggs or newly hatched larvae float to the surface where they spend their larval life. Shortly before metamorphosis to the adult form, the pelagic larvae (probably due to changes in their specific gravity [Tåning, 1918: 19–20, 149]) sink to deeper layers where metamorphosis is completed. Then the newly metamorphosed fishes join the adults in their diurnal vertical migrations, and their life span may be as long as four or five years. Since they feed almost exclusively on zooplankton, their vertical migrations have been correlated with the similar movements of their prey. Many myctophids, as they approach sexual maturity, develop sexually dimorphic

[1] Department of Biological Sciences, University of Southern California, Los Angeles, California.

characters in the form of various luminous structures.

The present study is limited to the North Atlantic with particular respect to *Lobianchia dofleini* and *Lobianchia gemellari*, the distribution patterns of which have recently been worked out by Nafpaktitis (Dana Report, in preparation). The purpose of the study is to illustrate the effects of expatriation on the gonads at the cellular level.

We are greatly indebted to Dr. Ned Feder of the Biology Department, Harvard University, for his technical advice and for allowing us to use many facilities in his laboratory. We are especially grateful to Dr. Giles W. Mead of the Museum of Comparative Zoology, Harvard University, for his kindness in reviewing the manuscript and offering valuable advice and criticism. L. V. Worthington and R. H. Backus of the Woods Hole Oceanographic Institution have generously given of their time for profitable discussions concerning several ideas in this paper. Partial support was obtained through grant GF 147, from the National Science Foundation to Harvard University in support of oceanic ichthyology.

MATERIALS

A list of the specimens from which gonads were removed and sectioned for the present work (sizes are in standard length) is as follows:

Lobianchia dofleini

One female, 33 mm, BLUE DOLPHIN, sta. RHB 450, 39°45′N, 71°08′W, July 16, 1953, 75 fms; one female, 32 mm, BLUE DOLPHIN, sta. RHB 467, 39°37′N, 70°58′W, August 19, 1953, 24 fms; one female, 36 mm, BLUE DOLPHIN, sta. RHB 471, 39°48′N, 70°34′W, August 23, 1963, varied depths; one female, 34 mm, ATLANTIS, sta. RHB 459, 41°05′N, 63°40′W, July 25, 1963, 340 fms; one female, 37 mm, CAPTAIN BILL, sta. RHB 904, 38°52′N, 71°55′W, October 10, 1962, 300 fms; one female, 33.5 mm, CHAIN, cruise 17, sta. RHB 801, 00 15′S, 18°40′W, April 26, 1961, 85 m; two females, 46 mm and 26 mm, CHAIN, cruise 17, sta. RHB 803, 09 27′N, 27 45′W, May 1, 1961, 275 m; one female, 32.5 mm, ATLANTIS II, cruise 13, sta. RHB 1004, 41°29′ N, 60°14′W, September 4, 1964, 330–395 m; one male, 33.6 mm, ATLANTIS II, cruise 13, sta. RHB 1005, 41°26.5′N, 59°01′W, September 4, 1964, 400–555 m; one female, 34.2 mm, ATLANTIS II, cruise 13, sta. RHB 1019, 41°53′N, 46°54′ W, September 9, 1964, 400–410 m; one female, 34 mm, ATLANTIS II, cruise 13, sta. RHB 1041, 39° 24′N, 27°11′W, September 21, 1964, 220–300 m; one female, 33 mm, GERONIMO, Bureau of Commercial Fisheries, Washington (BCFW) Cat. No. 324, 03°28′S, 00°14′W; one female, 27 mm, GERONIMO, BCFW Cat. No. 372, 31°49′N, 55° 19′W.

The above material is deposited at the Museum of Comparative Zoology, Harvard University.

One female, 36 mm, and one male, 32 mm, WALTHER HERWIG, sta. 103, 14°30′N, 55°19′ W, March 24, 1964, 900 m wire out. Institut für Seefischerei, Hamburg.

One female, 33 mm, CARYN, haul 23, 32°05.5′ N, 65°20′W, July 23, 1948, 1,500 m wire out; one female, 28 mm, CARYN, haul 56, 32°07′N, 64°37′ W, August 25, 1948.

The CARYN material is deposited at the Field Museum of Natural History, Chicago.

DANA material, deposited at the Danish Marine Biological Institute, Charlottenlund, Denmark, is listed below.

One female, 27.5 mm, sta. 1119 I, 36°08′N, 00° 30′W, September 23, 1921, 300 m wire out; one female, 36 mm, sta. 1131 I, 36°11′N, 02°12′W, October 2, 1921, 400 m wire out; one female, 27 mm, and one male, 27.5 mm, sta. 1134 II, 36°08′ N, 04°30′W, October 3, 1921, 300 m wire out; two females, 28.5 and 31 mm, sta. 1135 IV, 36°04′N, 05°05′W, October 4, 1921, 250 m wire out; one female, 40 mm, sta. 4157 IV, 44°01′N, 09°13′W, June 16, 1930, 300 m wire out; one female, 36 mm, sta. 4192 II, 39°57′N, 24°59′W, June 19, 1931, 600 m wire out; one female, 33 mm, sta. 4195 III, 41°55′N, 32°22′W, June 22, 1931, 300 m wire out; one female, 37 mm, sta. 4203 III, 49 49′N, 30°22′W, June 30, 1931, 300 m wire out.

Lobianchia gemellari

One female, 99 mm, CAPTAIN BILL II, sta. 19, 39°51′N, 71°13′W, June 23, 1952, 175–180 fms; one female, 101 mm, ATLANTIS, sta. RHB 462, 41°53′N, 64°23′W, July 28, 1953, 855 fms; two males, 37 and 57 mm, CHAIN, cruise 17, sta. RHB 808, 18°00′N, 39°00′W, May 5–6, 1961, 290 m; one female, 39 mm, CHAIN, cruise 17, sta. RHB 810, 20°55′N, 43°15′W, May 7, 1961, 495 m; one male, 45 mm, ATLANTIS II, cruise 13, sta. RHB 1020, 42°05′N, 46°29′W, September 9, 1964, 350–425 m; one female, 93 mm, ATLANTIS II, cruise 13, sta. RHB 1023, 43°16′N, 45°03′W, September 10, 1964, 520–700 m; one female, 50 mm, ATLANTIS II, cruise 13, sta. RHB 1026, 44°38′N, 43°55′W, September 11, 1964, 440 m; one female, 44 mm, ATLANTIS II, cruise 13, sta.

RHB 1044, 39°37′N, 31°10′W, September 26, 1964, 200–475 m.

The above material is deposited at the Museum of Comparative Zoology, Harvard University.

One female, 78 mm, WALTHER HERWIG, sta. 107, 14°30′N, 20°42′W, March 25, 1964, 900 m wire out. Institut für Seefischerei, Hamburg.

DANA material, deposited at the Danish Marine Biological Institute, Charlottenlund, Denmark, is listed below.

One female, 42 mm, sta. 1186 VI, 17°58′N, 64° 41′W, December 1, 1921, 1,000 m wire out; one female, 44 mm, sta. 1281 I, 17°43′N, 64°56′W, April 1, 1922, 1,000 m wire out.

METHODS

I. Postfixation. Acrolein postfixation proved unnecessary. Postfixed tissues were indistinguishable in histological sections from non-postfixed tissue. The postfixation procedure was as follows: the specimen was transferred from 72% ethanol to a solution of 10% acrolein in 72% ethanol, left overnight at 0°C, and then transferred to 100% ethanol and left at 0°C about 6 hours or longer. The latter step was repeated and then the tissue was dehydrated.

II. Dehydration. The specimens were transferred successively to the following solvents and left in them at 0°C for the indicated time:

(1) methyl cellosolve (ethylene glycol monomethyl ether) or 100% ethanol, 8–24 hours;
(2) n-propanol, 8–24 hours.

III. Embedding. Ovaries were impossible to section well in paraplast, a synthetic paraffin. Slightly better results were obtained with ester wax 1960, a very hard embedding medium, and polyester wax, a very soft (m.p. 37°C) embedding medium, which may be hardened during sectioning by being bathed in dry ice vapor. Both ester wax and polyester wax are described elsewhere (Steedman, 1960; Sidman, Mottla, and Feder, 1961).

Far better results were obtained with glycol methacrylate, a liquid monomer that polymerizes into a hard plastic when heated (Rosenberg *et al.*, 1960; Ashley and Feder, 1966). The "monomer mixture" contained 95 ml purified glycol methacrylate, 5 ml polyethylene glycol 200, and 0.15 g of catalyst (2,2′-azobis [2-methyl] propionitrile). Since the tissues were seldom larger than a few millimeters in diameter, one cc or less of 100% monomer mixture was sufficient to infiltrate them over a period of about two days. Just before polymerization, the tissues were stained for a few hours in a concentrated solution of acid fuchsin or safranin in 100% monomer mixture so that they could be seen in the hardened plastic for sectioning. Sections were cut at a thickness of one micron on a Porter-Blum microtome. Sections were floated on a drop of water on a glass slide and allowed to dry on the slide.

IV. Staining. Wax sections were stained in hematoxylin and eosin. Plastic sections were stained with toluidine blue or acid fuchsin followed by toluidine blue (Ashley and Feder, 1966). This was done by placing a drop of a concentrated aqueous solution of the dye on the section, and rinsing it in distilled water after the proper staining time, which was about four minutes or less for acid fuchsin and five minutes for toluidine blue. Stained sections were allowed to dry. Then they were mounted with permount and coverslipped.

V. Photographs. These were taken with Kodachrome II color film or Panatomic-X black-and-white film.

Lobianchia dofleini (Zugmayer)

Lobianchia dofleini (Fig. 1) is a stout little fish attaining a maximum size of about 48 mm in standard length and reaching sexual maturity at about 30 mm. Like its North Atlantic congener *L. gemellari*, *L. dofleini* shows striking secondary sexual dimorphism in the form of a series of luminous scale-like structures, which are located on the dorsal aspect of the caudal peduncle in males and on the ventral in females (Fig. 2).

L. dofleini is widely distributed in the North Atlantic (Fig. 3). It spreads across

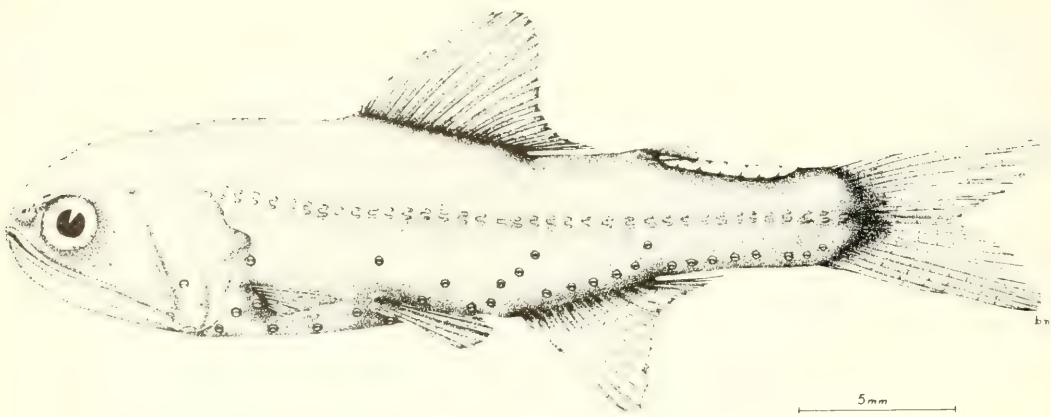


Figure 1. *Lobianchia dofleini* (Zugmayer, 1911). Male, 27 mm in standard length.

the ocean in a rather broad belt lying between the latitudes 26°N and 48°N. In spite of its wide distribution *L. dofleini* appears to have a reasonably well defined spawning range that includes the western Mediterranean Basin and the northeastern part of the North Atlantic, south of 48°N and east of 35 W.

This fish is not only widely distributed but is frequently taken in enormous numbers. With its wide distribution and abundance, its well developed swim bladder and its ability to undertake diurnal vertical migrations, it may well prove to be an important component of the deep scattering layers (D.S.L.), especially in the areas within its range where it is most numerous, i.e., off the coast of New England in the west, the western basin of the Mediterranean, and the adjacent waters of the North Atlantic in the east. Its properties as a sound scatterer have been discussed by Marshall (1951), and its probable involvement in the D.S.L. has been suggested by Hersey and Backus (1954).

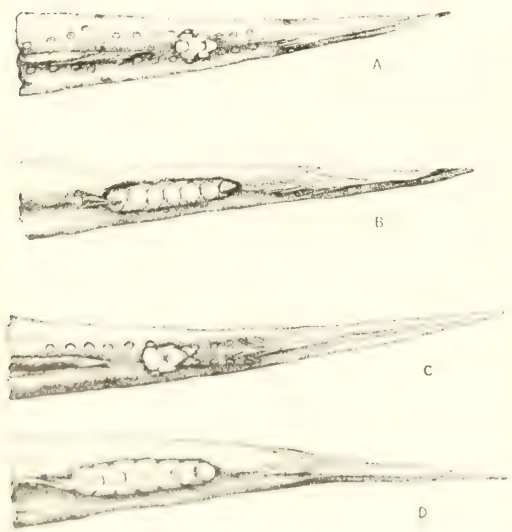


Figure 2. Luminous glands on caudal peduncle. *Lobianchia dofleini*: A, female; B, male. *L. gemellari*: C, female; D, male.

During the early stages of a systematic work on the species (Nafpaktitis, in preparation), it was noticed that females with ripe ova were becoming rare west of 30°W. This observation led to an extensive examination of many hundreds of specimens collected by various vessels in the western North Atlantic, west of 40°W, and north of 25°N. The results can be summarized as follows: (1) Not a single gravid female was found in collections made along and off the continental slope of the northeastern United States. At best, the gonads on gross examination appeared small and finely

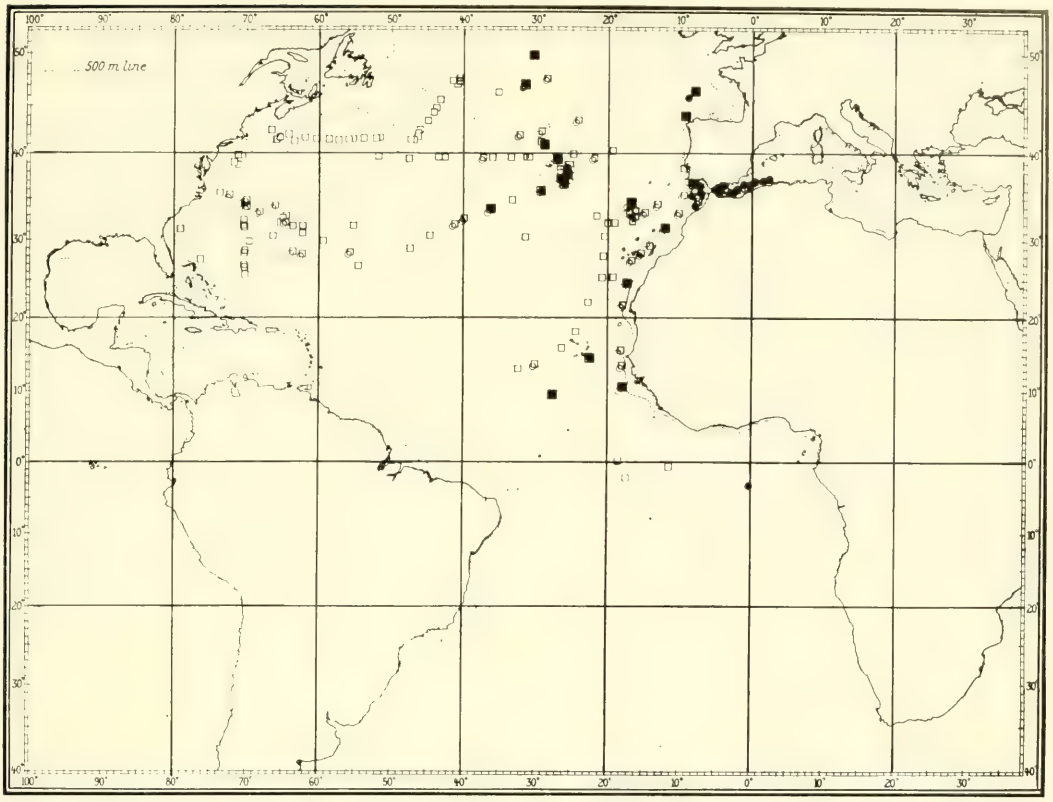


Figure 3. Distribution of *L. dofleini* in the North Atlantic. Solid dots represent gravid females; open squares, adults; solid squares, gravid females and adults; and circles, juveniles ≤ 12 mm in standard length.

granular, in spite of the fact that the caudal luminous structures in both sexes were fully developed. (2) In all collections along the continental slope and those north of 40°N, specimens smaller than 16 mm were absent. (3) Young stages, 11 mm to 12 mm, were found regularly along the R/V DANA transect from Cape Hatteras to Bermuda and from Bermuda to the Azores (Fig. 3).

The above findings aroused the suspicion that the population in the northwestern Atlantic consisted of expatriates which, under the hydrological conditions prevailing in that area, were incapable of reproducing. A histological examination of the gonads was subsequently undertaken.

Many specimens were sectioned, both from the expatriation area in the western North Atlantic and from the spawning grounds in the eastern North Atlantic, over a period of time extending throughout the summer and into early fall (see under *Materials*).

Results. The photomicrographs, Plate I, A and B, illustrate the differences between ovaries from specimens of *L. dofleini* taken in the reproductive area and those from specimens taken in the expatriation area. Expatriate specimens characteristically contained only oogonia and oocytes, while the relatively enormous yolk-filled eggs occurred only in ovaries of specimens from the spawning area. Expatriate oocytes contained no large yolk granules but did not appear abnormal. Their structure was entirely similar to that of a normal oocyte in

which vitellogenesis had not yet begun to a noticeable extent. Ovaries of females from the spawning area that are not preparing to spawn have many such oocytes.

Oocytes in early stages of development stain well with hematoxylin or toluidine blue. The developing oocyte grows greatly in size, the number of nucleoli increases, and a clear cytoplasmic zone separates the nucleus from a surrounding region of darker-staining cytoplasm, an effect which appears to be due to centrifugal migration of mitochondria and Golgi complexes (Droller and Roth, 1966). A faintly striated zona radiata, especially conspicuous in fish oocytes, can be seen in later stages of development. Eventually the oocyte is completely enclosed in a single layer of follicle epithelium and surrounded by thin connective tissue. Protein yolk stains well with acid fuchsin or eosin. The large, globular, non-staining cytoplasmic inclusions are apparently lipids (Chopra, 1960; Raven, 1961: 101–105; Droller and Roth, 1966).

Expatriate males had testes that contained mature sperm. The testis is composed of many lobules lined with germinal epithelium. Sperm are produced within these lobules and later move into a main duct. The entire structure is well vascularized and bound together by connective tissue (Hoar, 1957: 291). Mature sperm are small, hook-shaped cells that stain darkly with toluidine blue. Their delicate flagella are not preserved.

Discussion. Since the expatriate population is unable to reproduce itself, it must be maintained by regular transfusions of new individuals from the spawning area. The route over which these reinforcements arrive might be expected to follow the track of an ocean current, or series of currents, that integrate the expatriation area with the reproductive area. What is this route of constant reinforcement?

On the basis of hydrological evidence, L. V. Worthington of the Woods Hole Oceanographic Institution (Worthington, 1962) proposed a two-gyre system occupying the central and western North Atlantic (Fig. 4). The southern gyre, with Bermuda roughly in its center, extends to about 40° W. As it flows through the fringes of the spawning area, larvae and young stages are swept westward by it. Since the return flow of the southern gyre has an average velocity of about 10 cm per second (Worthington, personal communication), the young fishes could be transported from the fringes of the spawning area to the continental slope of North America in about one year. This time appears to be too long to account for the occurrence of 12 mm juveniles off Cape Hatteras, but little is known about fluctuations in the rate of transport and the duration of larval life. In view of present knowledge about the current system in the North Atlantic, the route proposed here seems to be the only feasible one. Under the influence of the westward flow, the expatriates will eventually reach the Gulf Stream. This current will rapidly carry them northward. Substantial numbers will enter the adjacent colder and less saline Slope Water (Iselin, 1936: 11) off the coast of the northeastern United States. Others

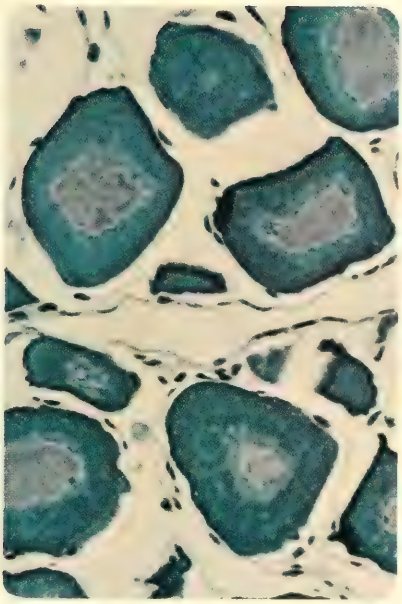
→

Plate I. A: Oocytes in the ovary of an expatriate *L. dofleini*, 34.2 mm in standard length; R/V ATLANTIS II, cruise 13, sta. RHB 1019, 41°53'N, 46°54'W, September 9, 1964, 400–410 m depth. Glycol methacrylate, toluidine blue, × 400.

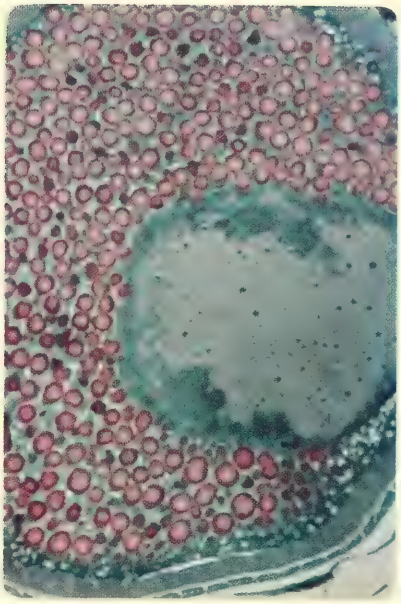
B: A single egg from the ovary of a specimen of *L. dofleini*, 31.0 mm in standard length, taken in the spawning area; R V DANA, sta. 1135 IV, 36°04'N, 05°05'W, October 4, 1921, 250 m wire out. Glycol methacrylate, acid fuchsin, toluidine blue, × 250.

C: Partial view of cross section of testis of expatriate *L. gemellari*, 45.0 mm in standard length, showing cell divisions but no sperm; R V ATLANTIS II, cruise 13, sta. RHB 1020, 42°05'N, 46°29'W, September 9, 1964, 350–425 m depth. Glycol methacrylate, toluidine blue, × 1,000.

D: Partial view of testis of *L. gemellari*, 57.0 mm in standard length, taken in the spawning area. Hook-shaped cells are mature sperm. R V CHAIN, cruise 17, sta. RHB 808, 18°00'N, 39°00'W, May 5–6, 1961, 290 m depth. Glycol methacrylate, acid fuchsin, toluidine blue, × 1,000.



A



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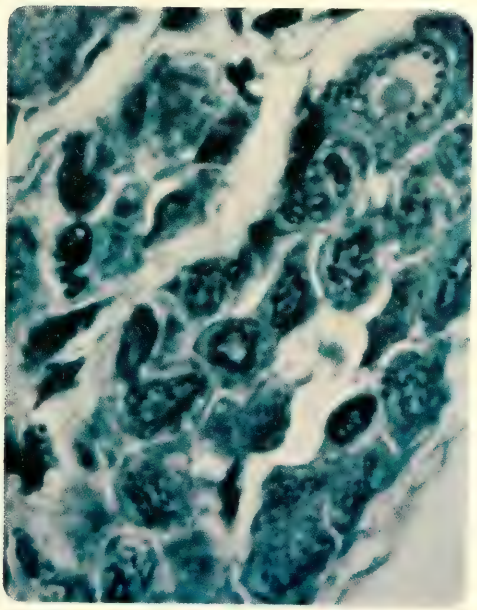

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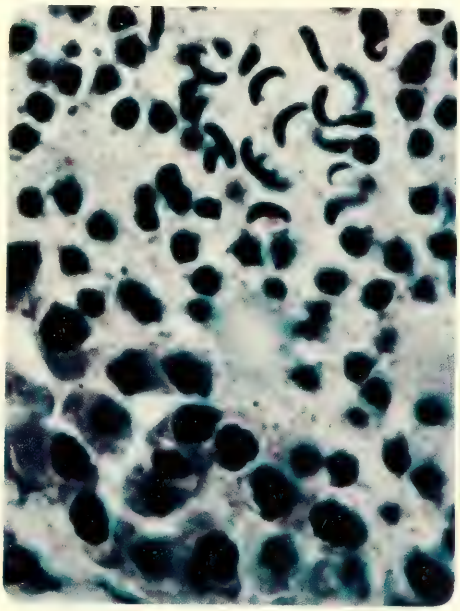

D

Plate I

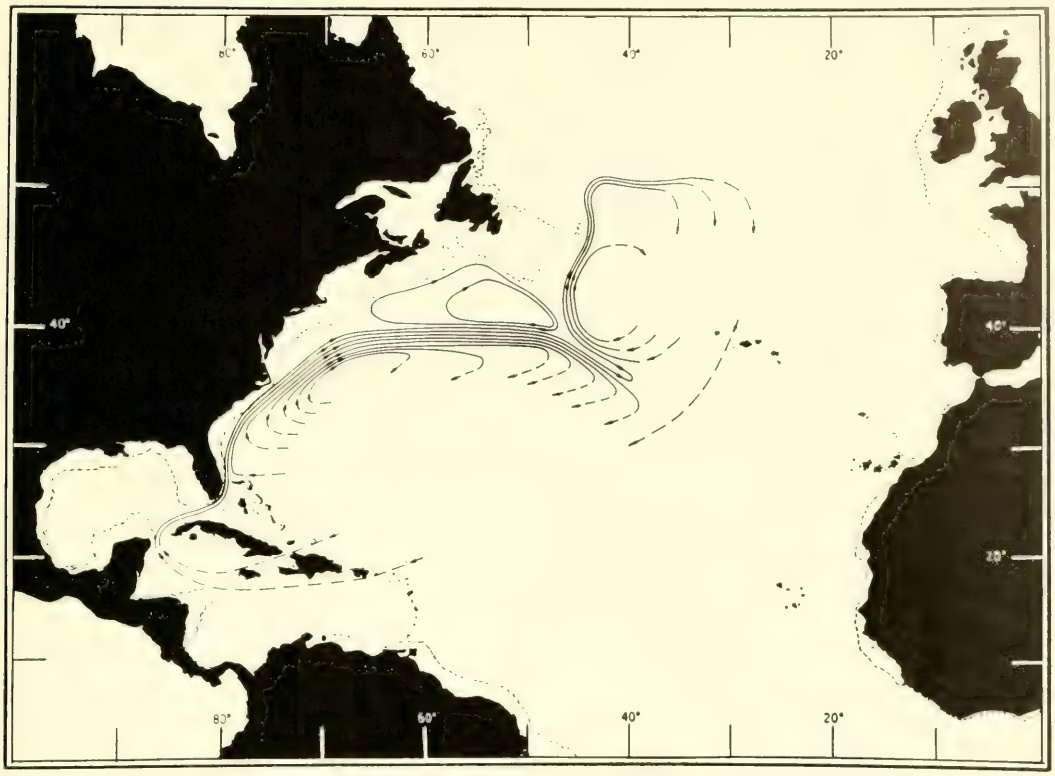

Figure 4. The two-gyre system proposed by Worthington (1962). Reproduced from Deep-Sea Research.

will remain in the Gulf Stream, while a few may follow the current until they return to the spawning grounds. In the expatriation area the young *dofleini*, apparently capable of adapting themselves to the physico-chemical factors, will grow to physical maturity. However, with ecological factors far from meeting the requirements of their reproductive physiology, these fishes will fail to reproduce.

There are remarkable differences between the temperature and salinity distributions in the expatriation area and the spawning area. Hjort (*in* Murray and Hjort, 1912: 444–445) wrote: "A peculiar feature is that all the [100 m] isotherms on the western side [of the North Atlantic] are quite close together, the water layers being squeezed between the oceanic subtropical waters from the south and the Labrador current from the north. All changes in temperature are therefore on the western side very sharp. On the eastern side the layers are spread out fan-wise, and as a consequence we may at a depth of 100 meters find the same temperature prevailing from north to south over wide areas . . ." The average temperatures at a depth of 200 m in the North Atlantic (Fig. 5) show a pattern very similar to that described by Hjort for the 100-meter isotherms. A temperature profile across the Atlantic at 40°N shows that there is a sharp convergence of isotherms above 2,000 m in a westward direction (Fig. 6). At the same latitude, the isohalines show a marked convergence from east to west (Fig. 7). Briefly, then, the variation in both temperature and salinity with depth is much

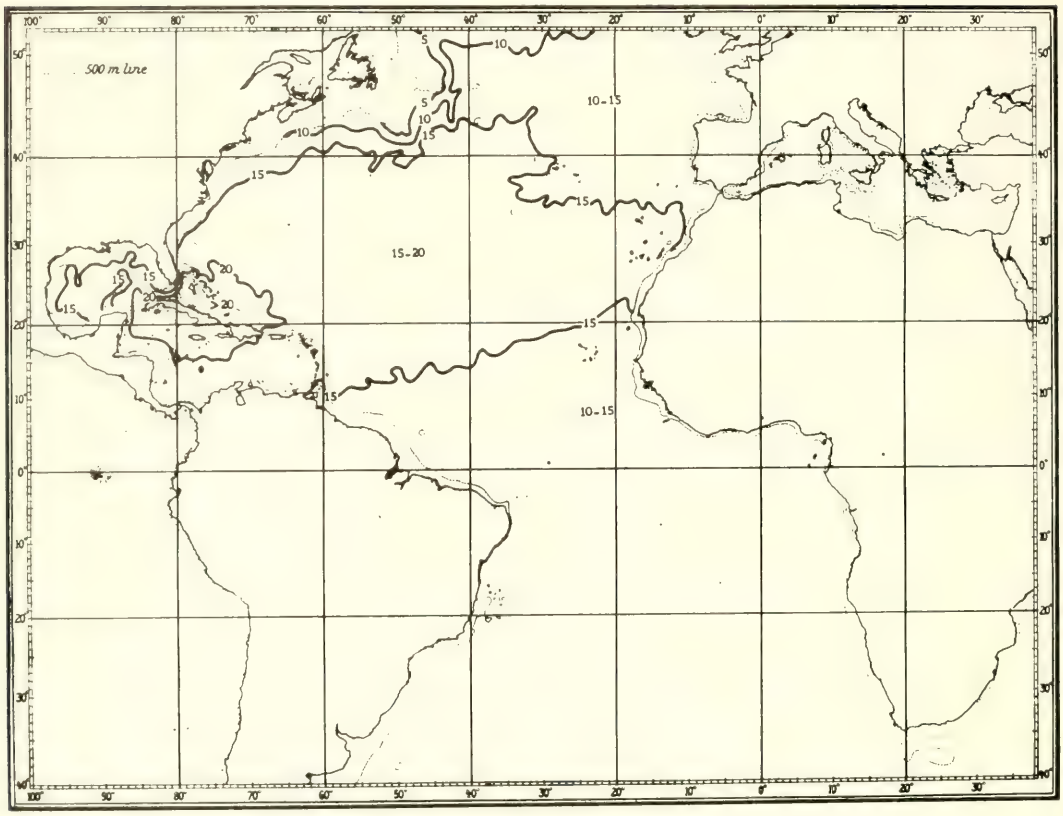

Figure 5. Average temperatures at a depth of 200 m in the North Atlantic. From Schroeder (1963, pl. 6).

greater in the expatriation area than in the spawning area. This variation is clearly reflected in the way the broadly spaced isotherms in the east converge, both horizontally and vertically, towards the northwestern North Atlantic.

The population of *Lobianchia dofleini* in the Slope Water off New England, which consists of adult individuals only, appears to be almost as dense as that in the spawning area. The Slope Water "is characterized by being the mixing zone, in the upper layers (down to 200 meters), for coastal water, which has escaped from over the

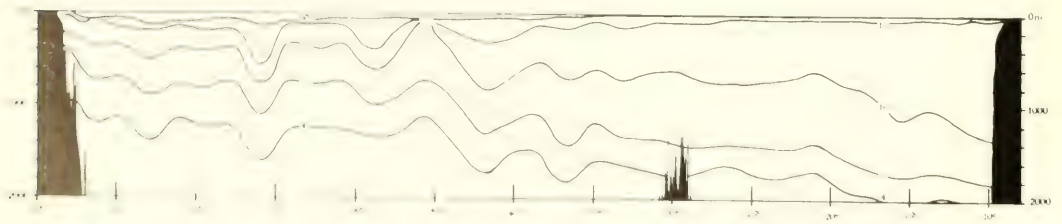

Figure 6. Temperature (°C) profile to a depth of 2,000 m at 40° N. from Georges Bank to Portugal (October 2–22, 1957). From Fuglister (1960: 41), intermediate isotherms omitted.

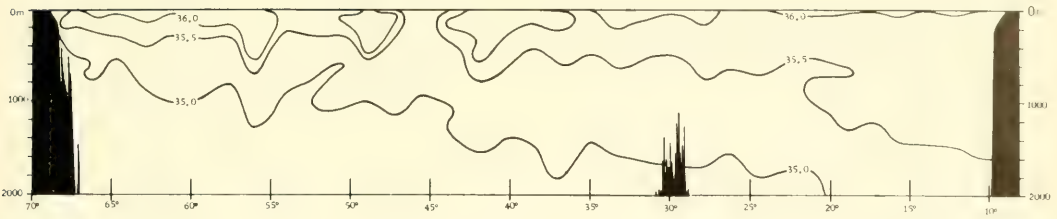

Figure 7. Salinity (‰) profile to a depth of 2,000 m at 40°N, from Georges Bank to Portugal (October 2–22, 1957). From Fuglister (1960: 79), intermediate isohalines omitted.

continental shelf, and Gulf Stream water, which has been carried west of the current's path" (Iselin, 1936: 11).

The broad stratification of both temperature and salinity in the water of the spawning area, and their much more narrow and less orderly distribution in the water of the expatriation area, suggest that stability of environment, within certain limits, may be a critical factor in the development of eggs.

Lobianchia gemellari (Cocco)

Expatriation from a subtropical environment to the same expatriation area inhabited by *L. dofleini* should produce similar or more severe effects in that expatriate. *L. gemellari* (Fig. 8), a species closely related to *L. dofleini*, confirms this expectation. Reaching sexual maturity at about 40 mm, *L. gemellari* is a somewhat larger fish than *L. dofleini*. It has a wide distribution, but is most abundant within a broad belt of warm water in the central North Atlantic (Fig. 9). Its spawning area includes the Caribbean Sea and adjacent waters.

Expatriation produces more drastic effects in *L. gemellari* than in *L. dofleini*. Not only are gametes of both sexes prevented from growing normally, but even secondary sexual characters fail to develop fully. Expatriate males are generally indistinguishable from expatriate females, although a few specimens show traces of sexually dimorphic luminous tissue on the

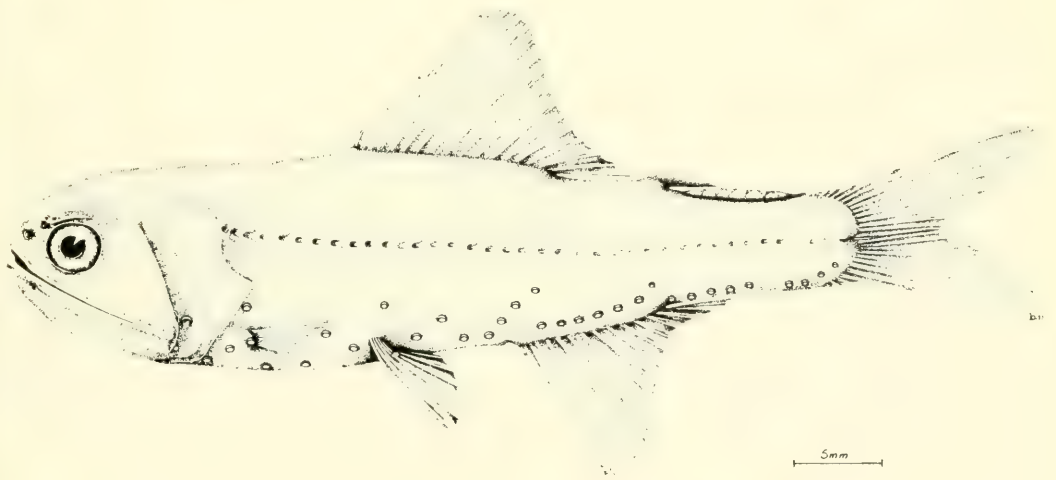

Figure 8. *Lobianchia gemellari* (Cocco, 1838). Male, 47.6 mm in standard length.

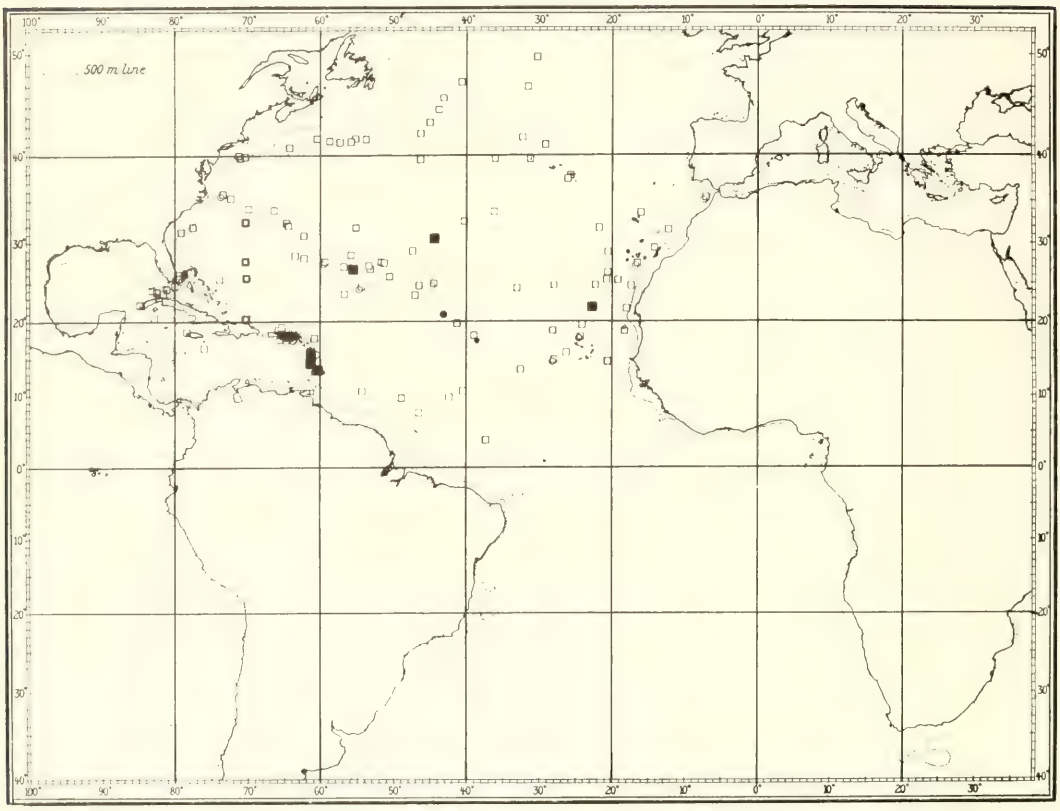

Figure 9. Distribution of *L. gemellari* in the North Atlantic. Solid dots represent gravid females; open squares, adults; solid squares, gravid females and adults; and circles, juveniles ≤ 12 mm in standard length.

caudal peduncle. Accordingly, histological examination was necessary to determine sex in most expatriate specimens of *L. gemellari*, for the gonads in both sexes were thread-like whitish structures. Ovaries in some specimens were evident from a barely visible granular consistency. In contrast, the ovaries of mature but non-spawning females of the reproductive area were far larger, yellow, and noticeably granular.

Results. Histological sections of ovaries from gravid females caught in the spawning area, show many large yolk-filled eggs and some growing oocytes (Plate II, A).

→

Plate II. A: Several oocytes in different stages of development in the ovary of a specimen of *L. gemellari*, 42.0 mm in standard length, taken in the spawning area; R V DANA, sta. 1186 VI, 17°58'N, 64°41'W, December 1, 1921, 1,000 m wire out. Glycol methacrylate, acid fuchsin, toluidine blue, × 100.

B: Very small oocytes in the ovary of an expatriate *L. gemellari*, 50.0 mm in standard length; R V ATLANTIS II, cruise 13, sta. RHB 1026, 44°38'N, 43°55'W, September 11, 1964, 440 m depth. Glycol methacrylate, acid fuchsin, toluidine blue, × 1,000.

C: Cross section through a lobule in the testis of a specimen of *L. dofleini*, 27.5 mm in standard length, from the spawning area; R V DANA, sta. 1134 II, 36°08'N, 04°30'W, October 3, 1921, 300 m wire out. Glycol methacrylate, toluidine blue, × 1,000.

D: Cross section through a lobule in the testis of an expatriate *L. dofleini*, 33.6 mm in standard length; R V ATLANTIS II, cruise 13, sta. RHB 1005, 41°26.5'N, 59°01'W, September 4, 1964, 400–555 m depth. Glycol methacrylate, toluidine blue, × 1,000.

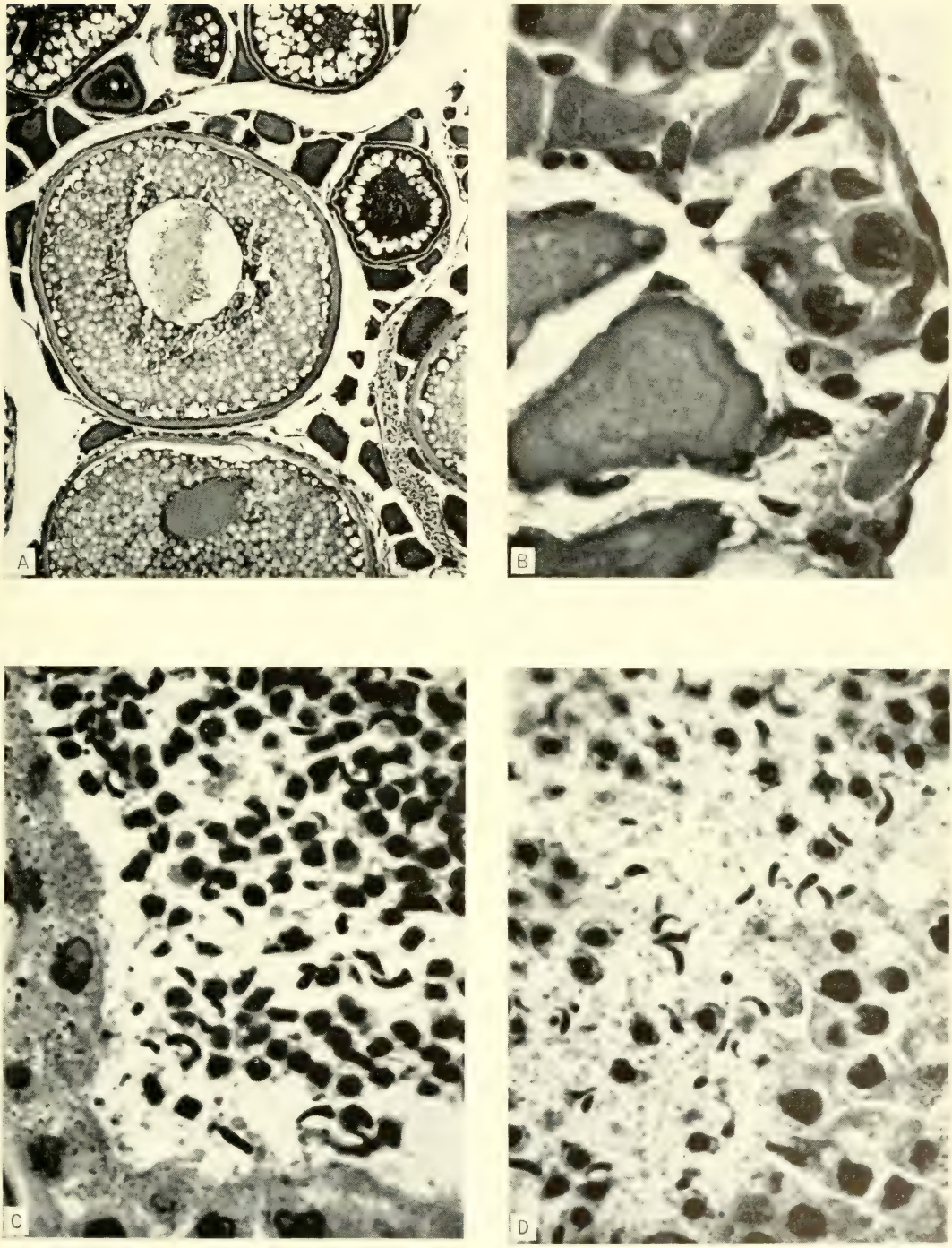

Plate II

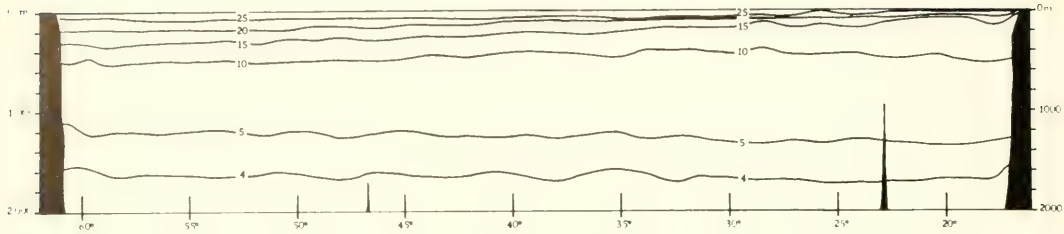

Figure 10. Temperature (°C) profile to a depth of 2,000 m at 16°N, from Guadeloupe to French West Africa (November 13–29, 1957). From Fuglister (1960: 31), intermediate isotherms omitted.

The testes of males from the reproductive area contained large numbers of sperm (Plate I, D). Expatriate females had ovaries that contained extremely few oocytes, and even these were very small (Plate II, B) in comparison to the oocytes in the ovaries of females from the reproductive area. In expatriate ovaries the oocytes were similar in appearance to the smallest oocytes in a normal ovary. Expatriate testes did not contain mature sperm (Plate I, C). However, both testes and ovaries of expatriate *gemellari* showed a great number of cell divisions, in spite of the relatively minute size of these gonads and their superficial appearance of inactivity. Chromosomes were easily visible when stained with toluidine blue.

Discussion. The process of expatriation for this species is swift and short. The Florida Current, which flows through the Straits of Florida at a maximum velocity of 160 cm per second (74.5 miles per day) at the center of the current (Sverdrup *et al.*, 1942: 673–674), can easily initiate expatriation. The Gulf Stream, which is continuous with this current at Cape Hatteras, can speed the expatriates northward more than 60 miles per day (computed from velocities given by Sverdrup *et al.*, 1942: 675).

The differences in the expatriate environment are more pronounced for *L. gemellari* than for *L. dofleini*. As the temperature profiles at 16°N and 40°N indicate, the waters within the spawning area are warmer, and their temperatures vary less with depth. For example, at 16°N the temperatures at 200 m range from 15°C to 20°C (Fig. 10), but at 40°N it is generally colder than 15° C at this depth. The horizontal temperature distribution at 200 m depth (Fig. 5) also shows the same differences.

Other examples

Several species of the myctophid genus *Diaphus* are expatriated in the same way as *L. gemellari* and should provide further examples of the effects of expatriation. *Diaphus mollis* and *D. effulgens* from subtropical and warm central North Atlantic waters, *D. elucens* and *D. lucidus* from tropical waters have all been caught in the same expatriation region inhabited by *L. dofleini* and *L. gemellari*. It is very probable that not all expatriate species are reproductively affected in the same way as *L. dofleini* and *L. gemellari*. Death of gametes or unsuccessful development in very early stages are some other possible effects of expatriation.

CONCLUSION

The area in which a species can exist may be much larger than the area in which it can spawn. Unlike eels, salmon, or herring—which migrate far from their spawning grounds but return as part of the regular life cycle—expatriates return to the spawning area only by chance. The majority of expatriates live vegetatively in an alien environment, for which their tolerance may vary. Expatriates of *L. dofleini* are vigorous

and numerous and show normal sexual dimorphism, but cannot reproduce. *L. gemellari* expatriates are affected more severely; reproduction is impossible and secondary sexual dimorphism is reduced or nonexistent.

The effects of expatriation may be far-ranging. Within the species from which expatriates are drawn, it may relieve population density. Furthermore, the possible evolutionary implication of expatriation should not be overlooked. Considering that species are more or less localized in water masses which are defined by their physical, chemical, and biological characteristics, it is conceivable that there will occur occasional mutant expatriates which are pre-adapted to the expatriate environment. Following restriction of gene flow, selection pressures in the new environment will initiate and advance speciation. "Although more subtle than nearshore or terrestrial barriers to or means of dispersal, boundaries and colonization routes in the open ocean have helped elaborate the immense and varied bathypelagic fauna" (Ebeling, 1962: 148).

The phenomenon of expatriation seems to be more widespread than has been thought. It should be looked for and expected wherever ocean currents flow through different water masses.

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(Received 26 September 1966.)

Bulletin OF THE
Museum of
Comparative
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Delimitation of the Genus *Ceracis* (Coleoptera: Ciidae) with a Revision of North American Species

JOHN F. LAWRENCE

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 6
NOVEMBER 14, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

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Breviora 1952–
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DELIMITATION OF THE GENUS *CERACIS* (COLEOPTERA: CIIDAE) WITH A REVISION OF NORTH AMERICAN SPECIES

JOHN F. LAWRENCE

INTRODUCTION

The genus *Ceracis*, as it is here delimited, includes about 40 described species, occurring primarily in the New World. Mellié (1848) originally proposed the name for a subgenus of *Ennearthron*, the species of which were characterized by having 8, instead of 9, antennal segments. In the present paper, the limits of this genus are expanded to include species which may have 8, 9, or 10 antennal segments, but which share a number of prosternal and tibial characters to be discussed below. Although a complete revision is not possible at this time, some of the more apparent synonymies are included in the generic treatment, and detailed accounts are given for those species occurring in the United States and Canada.

Since the genera *Ennearthron* and *Ceracis* have been confused in the literature, it would be useful to outline briefly the history of both concepts. The genus *Ennearthron* was described by Mellié in 1847, but no species names were included. In 1848, Mellié placed 15 species in the genus, 5 of which comprised a new subgenus, *Ceracis*. The nominate subgenus was divided into 2 groups: species with the elytra "pubescentes" and those with the elytra "glabres." The first group included *E. cornutum* (Gyllenhal), *E. affine* (Gyllenhal), and *E. fronticornis* (Panzer). *E. cornutum*, which was later designated as type species by Desmarest (1860), has the prosternum somewhat tumid with a broad intercoxal process and the protibia with a single tooth at the apex; except for the antennal segmentation, it closely resembles many species of *Cis*. *E. affine* and *E. fronticornis* differ from *E. cornutum* in having the prosternum somewhat concave and the protibial apex bearing several small spines; these two species are now placed in the genus *Sulcacis* Dury (=*Entypus* Redtenbacher, not Dahlbom) (Lohse, 1964; Lawrence, 1965). The remaining 7 species form a more compact group in which the surface appears glabrous (actually covered with very short and fine hairs), the prosternum is concave, the intercoxal process laminate, and the protibial apex expanded and bearing several spines. These species differ from those placed in *Ceracis* only in the number of antennal segments.

Since Mellié's monograph was the first and only world revision of the family Ciidae, no further attempts were made to clarify these generic concepts. Lacordaire (1857) considered *Ceracis* to be generically distinct from *Ennearthron*, and subsequent authors added new species to both genera, usually on the basis of antennal segmentation alone. Most North American workers applied the name *Ennearthron* only to those species falling into Mellié's second group, and other forms with 9-segmented antennae were placed in different genera, such as *Dolichocis* Dury and *Plesiocis* Casey. The only exceptions are *Ennearthron transversatum*, *E. annulatum*, and *E. pallidum*, all described by Kraus (1908); these three

forms resemble the species of *Orthocis* Casey and may represent a distinct genus. European workers placed more weight on antennal characters and included a number of diverse forms within the genus *Ennearthron*.

At the present time, 54 nominal species of *Ennearthron* exist in the literature; in the following treatment, 26 of these (representing 16 valid species) are removed and placed in the genus *Ceracis*. The remaining species of *Ennearthron* still form a rather heterogeneous group. Some of them represent typical species of *Cis*, in which antennal segments have been miscounted, while the others represent at least 7 distinct phyletic lines, in which the number of antennal segments has become reduced. Several of these species probably should be placed in the genus *Cis*, in spite of the antennal segmentation, but further study will be necessary to determine their relationships. Of the 25 nominal species of *Ceracis*, 5 are removed and the remainder represent 15 valid species. These will be discussed in more detail below.

ACKNOWLEDGMENTS

I am indebted to the following individuals and institutions for making their collections available to me: Academy of Natural Sciences of Philadelphia, Philadelphia, Pa. (H. J. Grant); American Museum of Natural History, New York, N. Y. (J. Rozen, P. Vaurie); Bernice P. Bishop Museum, Honolulu, Hawaii (J. L. Gressitt, G. A. Samuelson); Brigham Young University, Provo, Utah (V. M. Tanner, S. L. Wood); British Museum (Natural History), London, England (J. Balfour-Browne, R. Pope); California Academy of Sciences, San Francisco, Calif. (H. B. Leech); California Insect Survey, University of California, Berkeley, Calif. (J. Powell, P. D. Hurd); Bureau of Entomology, California State Department of Agriculture, Sacramento, Calif. (M. Wasbauer); Entomology Research Institute, Canada Department of Agriculture, Ottawa, Canada (H. Howden, W. J. Brown); Carnegie Museum, Pittsburgh, Pa. (G. E. Wallace); Chicago Natural History Museum (Field Museum), Chicago, Ill. (H. S. Dybas, R. Wenzel); Cincinnati Museum of Natural History, Cincinnati, Ohio (C. Oehler, R. Dury); Jim F. Cornell, Corvallis, Oregon; Department of Entomology, Cornell University, Ithaca, N. Y. (W. L. Brown); Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil (H. Reichardt, U. Martins); Henry Howden, Ottawa, Canada; Illinois Natural History Survey, Urbana, Ill. (H. H. Ross, L. K. Gloyd); Institut Royale des Sciences Naturelles de Belgique, Brussels, Belgium (R. Damoiseau); Muséum d'Histoire Naturelle, Geneva, Switzerland (C. Besuchet); Muséum National d'Histoire Naturelle, Paris, France (A. M. Villiers); Museum of Comparative Zoology, Cambridge, Mass. (P. J. Darlington); Department of Entomology, Purdue University, Lafayette, Ind. (L. Chandler); Joe Schuh, Klamath Falls, Ore.; United States National Museum, Smithsonian Institution, Washington, D. C. (P. J. Spangler, J. M. Kingsolver, O. L. Cartwright); University of Alberta, Edmonton, Alta. (D. Whitehead); Department of Entomology, University of Arizona, Tucson, Ariz. (F. G. Werner); Department of Entomology, University of California, Davis, Calif. (A. T. McClay); Snow Entomological Museum, University of Kansas, Lawrence, Kansas (G. W. Byers); Burke Memorial Museum, University of Washington, Seattle, Wash. (M. H. Hatch).

Sincere thanks are extended to the following specialists for their determinations of fungus specimens: R. L. Gilbertson and J. Lowe, Department of Forest Botany and Pathology, State University College of Forestry, Syracuse, N. Y.; J. A. Stevenson, National Fungus Collection, Plant Industry Section, Beltsville, Md.; L. Bonar and I. Tavares, University of California Herbarium, Berkeley, Calif.

Thanks are also due to the following individuals who have made a special effort to collect specimens of Ciidae with their

host fungi in various parts of North and Central America: R. Andrews, P. D. Ashlock, R. C. Banks, P. de Benedictis, L. J. Bottimer, J. T. Doyen, R. C. Graves, D. H. Janzen, A. Laska, M. Lundgren, C. W. and L. O'Brien, C. Oehler, C. Parsons, J. A. Powell, J. R. Powers, A. G. Raske, M. and K. Tauber.

I am grateful to R. A. Crowson, R. C. Graves, R. L. Gilbertson, M. Nobles, and K. Southern (Paviour-Smith), for discussing with me problems of ciid classification and host specificity, and to P. J. Darlington, Jr., and E. Mayr for the critical reading of this manuscript.

I am indebted to the American Museum of Natural History and to M. Cazier and R. Archbold for the help and hospitality offered during my stay at the Southwest Research Station, Portal, Arizona, and the Archbold Biological Station, Highlands Co., Florida.

I also wish to thank Mrs. M. Catron, K. Davis, and K. Pearson for illustrations and technical assistance.

Part of this research was conducted with the aid of a National Science Foundation Grant (GB–4743), National Science Foundation Summer Fellowships, Woodrow Wilson Foundation Fellowship, and Grants-in-aid from the University of California Committee on Research, Woodrow Wilson Foundation, and the Society of the Sigma Xi.

METHODS AND TERMINOLOGY

Taxonomic characters. Color is of limited usefulness as a diagnostic character in this family because of the relatively long period of time between eclosion and the attainment of full pigmentation, during which tenerals are abundant in the population. It is even less useful in this genus because of its variation in fully pigmented adults. When color is used in descriptions, it is stated in simple terms, and words like "fuscous" and "piceous" are avoided. The texture of the pronotum and elytra, which is diagnostic for some species, may be described as distinctly granulate, lightly granulate, or smooth, and the surface sheen varies from dull to shiny accordingly. The vestiture is fairly constant throughout the genus, and differences in the lengths of the fine hairs are too small to be noted in the descriptions.

Head characters are used primarily for males (see below). The vertex is defined as the entire area between the eyes from the frontoclypeal ridge to the concealed occiput. In most Ciidae, the area in the vicinity of the frontoclypeal suture forms a ridge extending from the edge of one eye to the other. This is called the frontoclypeal ridge, since it contains parts of both the frons and the clypeus.

The antennae may be 8-, 9-, or 10-segmented, depending upon the number of segments between the scape and the 3-segmented club. Ratios between various segments may be of value at the specific level, but in this treatment only the ratio of segment III to segment IV has been used.

The pronotum varies considerably between species in size, shape, and punctation. The disc in some species is declined. The punctures are fairly evenly distributed, but there is some variation in the distances between them. Some measure of the coarseness and density of the pronotal punctation is obtained by comparing the average puncture diameter to the length of the scutellar base and the distances between punctures to the diameter of a puncture. Other pronotal characters are found only in males and will be discussed below.

The elytra also vary in size, shape, and punctation. The sides may be parallel for most of their lengths or rounded. The elytral punctation may be single—consisting of punctures uniform in size and distribution, or dual—composed of punctures of variable size and usually falling into 2 distinct size classes. When the punctation is dual, the larger punctures (or both sizes) are occasionally seriate, forming distinct rows. The coarsenesss and density of the larger elytral punctures may be compared

to that of the pronotal punctures. The diameter of an elytral puncture, though, is often difficult to measure, because of shadow effects caused by variation in the slope of the sides of the puncture. The shape of the elytra, as determined by a length–width ratio may be used as a diagnostic character, since it does not differ between the sexes.

Prosternal characters are used only in the generic description. The term "body of prosternum" refers to that part in front of the coxal cavities, and this is continued posteriorly as the laminate intercoxal process. The postcoxal process is a mesial continuation of the pronotal hypomeron.

There is some variation in the numbers of spines on the apex of the protibia, but this variation is intraspecific as well as interspecific. The exact number of spines is difficult to determine since the spines grade into fine setae toward the inner angle. For these reasons, protibial characters were not used in the species descriptions or diagnoses.

The metasternum varies somewhat in its shape, and the metasternal suture varies in length as compared to the median length of the sternal plate. The abdomen also varies somewhat in length, but has not been used. The setigerous pore in the middle of sternite III is found in males only. Characters involving the 8th sternite of the male and the aedeagus have not been used in species descriptions, because there seems to be little variation here between species. This is in marked contrast to genital characters in the genus *Cis*, which are often diagnostic for species or species groups. In the generic description, the terms tegmen and median lobe are used, following Sharp and Muir (1912).

Secondary sexual characters. In all species of the genus, the males are characterized by having a setigerous pore on the first visible abdominal sternite (sternite III). This pore, which may be circular or transversely oval, smaller or larger in size, distinctly or indistinctly margined, and located at the middle of the sternite or posterad of this, is a useful diagnostic character for males, since it does not appear to vary within a species. In indicating the size and position of the pore, the term "body of sternite" refers to that portion behind the intercoxal process.

The males of most species differ from females also in the shape of the pronotum, the development of the pronotal apex, and the structure of the frontoclypeal ridge. The use of these characters to separate species, however, requires a good deal of caution and has led to the formation of a number of synonyms in the past. Each of these characters varies within a species, and the variation may be considerable. The shape of the pronotum is the least variable, if one excludes the development of the apex. Larger male specimens often have the pronotum expanded laterally and the sides subparallel, whereas smaller males and all females have the sides more rounded and not expanded. The apex of the pronotum may be rounded or weakly emarginate in the males of some species, produced forming two tubercles, teeth, or horns in others, and forming an emarginate lamina in others. The teeth or horns vary in size and may be parallel or diverging. In all of these species, the smaller males have weakly developed pronotal characters, and the smallest specimens can barely be distinguished from females on the basis of this character alone. The frontoclypeal ridge is simple and rounded or truncate in some species, and variously produced in others, forming an emarginate lamina, two tubercles or horns, or an elongate median horn. These characters also vary within a species, and in smaller males they are barely developed.

The matter is further complicated by the fact that the pronotal and frontoclypeal characters vary allometrically, so that the length of a pronotal lamina increases logarithmically with an arithmetic increase in another character such as elytral length. The curious situation then arises that the form which "characterizes" a given species,

or that which most easily distinguishes it from related species, is present only in the largest males, which comprise a minority of the population.

Measurements and ratios. The pronotal length (PL) is measured along the midline, and in males it includes the horns or laminae. The pronotal width (PW) is the greatest width. The elytral length (EL) is taken just to one side of the midline from the base of the scutellum to the elytral apices. The elytral width (EW) is the greatest width. The total length is the sum of PL and EL and does not include the head; it is given in mm. For one sample of each species, the range, mean, and standard error of the mean are given for the total length and for the following ratios: TL EW, PL/PW, EL/EW, EL/PL. In the description, these ratios are given for a male and a female (holotype and allotype or plesiotypes), and the statistical treatment is included in the section on variation. Ratios are used in the keys only when there is very little or no overlap between species or groups of species.

Locality data. Because of the large numbers of specimens examined, complete data are given only for types or plesiotypes. For each species, the total number of specimens examined is included, followed by a list of localities, and the institutions or private collections providing the material for study. The localities are grouped according to general area (Canada, United States, Mexico, Central America, West Indies), subgrouped alphabetically by province, state, or country, and listed alphabetically within each. The following abbreviations are used to indicate the sources of material: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; BBM, Bernice P. Bishop Museum; BMNH, British Museum (Natural History); BRUS, Institut Royale des Sciences Naturelles de Belgique; BYU, Brigham Young University; CAS, California Academy of Sciences; CDA, California State Department of Agriculture; CIN, Cincinnati Museum of Natural History; CM, Carnegie Museum; CNC, Canadian National Collection; CNHM, Chicago Natural History Museum (Field Museum); CU, Cornell University; GEN, Muséum d'Histoire Naturelle, Geneva; HH, Henry Howden Collection; INHS, Illinois Natural History Survey; JFC, J. F. Cornell Collection; JFL, J. F. Lawrence Collection; JS, Joe Schuh Collection; KU, University of Kansas; MCZ, Museum of Comparative Zoology; MNHN, Muséum National d'Histoire Naturelle, Paris; PURD, Purdue University; UAL, University of Alberta; UAZ, University of Arizona; UCD, University of California, Davis; CIS, California Insect Survey; USNM, United States National Museum; UW, University of Washington.

Host data. The host fungi are listed according to the apparent order of preference. For each fungus species, the total number of records is given, and this is followed by the number of apparent breeding records (in parentheses). For the purposes of this study, a breeding record is any collection with 10 or more adults or 1 or more tenerals or immatures. Only those collections in which the fungus was determined by a known specialist (my own records and those of R. C. Graves and H. S. Dybas) are included as breeding records. The nomenclature follows that of Overholts (1953), Lowe (1957, 1966), and Lowe and Gilbertson (1961a, 1961b), but the generic placements are those of the latter two authors. Records were obtained by collecting specimens in the field or rearing them in the laboratory. Identifications were made by several specialists mentioned above in the acknowledgments. Further information on the host fungi is contained in the section on North American *Ceracis*.

GENERIC TREATMENT

Subfamily CIINAE Leach
Genus *CERACIS* Mellié

Ennearthron (*Ceracis*) Mellié, 1848: 375. Type species, by present designation, *Ennearthron* (*Ceracis*) *sallei* Mellié, 1848: 377.

Ceracis Mellié; Lacordaire, 1857: 553; Jacquelin DuVal, 1857: 246; Reitter, 1878: 37; Gorham, 1883: 223 (in part); Gorham, 1886: 359; Horn, 1894: 391; Gorham, 1898: 332 (in part); Casey, 1898: 90; Blatchley, 1910: 900; Dalla Torre, 1911: 25; Pic, 1916a: 20; Dury, 1917: 27; Lesne, 1917: 192; Leng, 1920: 247; Pic, 1922: 2–3; Zimmerman, 1942: 51; Blackwelder, 1945: 549; Arnett, 1962: 829.

Cerasis Demarest, 1860: 261. Incorrect subsequent spelling.

Ceratocis Gemminger and Harold, 1869: 1800. Unjustified emendation.

Bostrichus, — Bosc, 1791: 6; Bosc, 1792: 259.

Cis, — Ziegler, 1845: 270; Mellié, 1848: 236 (in part); Blair, 1935: 295 (in part).

Ennearthron, — Mellié, 1847: 110 (in part); Mellié, 1848: 360 (in part); Jacquelin DuVal, 1857: 245 (in part); Lacordaire, 1857: 552 (in part); LeConte, 1867: 58; Gemminger and Harold, 1869: 1799 (in part); Abeille de Perrin, 1874: 80 (in part); Reitter, 1878: 36; Casey, 1884: 36; Casey, 1898: 87; Reitter, 1902: 59 (in part); Fauvel, 1904: 163; Blatchley, 1910: 900; Dalla Torre, 1911: 23 (in part); Pic, 1916a: 19 (in part); Dury, 1917: 22 (in part); Leng, 1920: 247 (in part); Brethes, 1922: 303; Scott, 1926: 35 (in part); Pic, 1939: 18; Blackwelder, 1945: 549 (in part); Miyatake, 1954: 55 (in part); Arnett, 1962: 829 (in part); Hatch, 1962: 234.

Octotemnus, — Tanner, 1934: 47.

Scolytocis, — Blair, 1944: 126.

Vestocis (in part), — Dury, 1917: 15; Leng, 1920: 247; Arnett, 1962: 829.

Xylographus, — Gorham, 1886: 355 (in part).

Diagnosis. This genus may be distinguished from other members of the Cisnae by the oval to elongate and cylindrical body form, the narrow lateral pronotal margin and obtuse or rounded anterior pronotal angles (Fig. 1), the concave prosternum and laminate prosternal intercoxal process (Figs. 2–3), the apically expanded protibia, which bears several spines along the outer apical angle (Fig. 4), the strongly convex metasternum with the suture short or absent (Fig. 5), the vestiture consisting of very short and fine hairs, and the form of the aedeagus (Figs. 9–10).

Description. Size relatively small, TL ranging from about 0.80 to 2.20 mm. Form oblong and suboval to elongate and cylindrical, strongly convex. Vestiture consisting of very short and fine suberect or decumbent hairs. Head strongly declined, partly to almost completely concealed from above by pronotum; vertex flat or impressed, often with a median tubercle or boss and occasionally with an erect horn; frontoclypeal ridge in male usually produced and elevated, forming a lamina which may be truncate or emarginate, the apex of the lamina often with 2 lateral pilose patches, occasionally forming 1 or 2 distinct tubercles or horns; genal ridge weakly elevated and subcarinate, forming a shallow antennal fossa between it and the eye. Antennae 8- to 10-segmented, with a large, loose, 3-segmented club, each club segment bearing 4 sensory pores; maxilla with mediostipes subtriangular, lacinia subterminal, subequal to galea, which is terminal, short and broad, terminal segment of maxillary palp usually narrow and elongate; prementum somewhat elongate, terminal segment of labial palp shorter and narrower than penultimate segment. Pronotum transverse to elongate, narrowly margined laterally and posteriorly, the lateral margins not visible for their entire lengths from above, anterior angles obtuse, rounded or subangulate, not produced forward (Fig. 1); anterior edge in male rounded, or produced, forming a lamina or 1 or 2 teeth or horns, the apex of each horn or the apicolateral angles of lamina often with a pilose patch above. Scutellum usually broadly triangular. Elytra longer than broad, the sides rounded or subparallel; punctation single or dual, the punctures uniform, confused, or seriate. Prosternum concave or very slightly tumid mesially, always concave or biconcave in cross-section, body shorter than intercoxal process, which is laminate, less than 0.12 × as wide as a procoxal cavity; postcoxal processes acute, extending mesad for about 0.80 of coxal width, leaving narrowly open behind the procoxal cavities, which are about 0.50 × as long as wide (Figs. 2–3). Protibia strongly expanded at apex, the outer apical angle forming a rounded process, which bears several spines, grading into setae

toward the inner angle (Fig. 4). Metasternum strongly convex; suture less than 0.50 × as long as median length of sternum, usually very short or absent (Fig. 5). Meso- and metatibiae slightly expanded and spinulose at apices. Abdomen somewhat shorter than wide at base, strongly convex; sternite III in male with median, setigerous pore, which may be circular (Fig. 6) or transversely oval (Fig. 7); sternite VIII in male short and broad, base bisinuate, apex emarginate, the apical angles rounded, each with a group of setae (Fig. 8). Tegmen moderately elongate, rounded basally, broadly and deeply emarginate apically, lightly pigmented basally and laterally (Fig. 9); median lobe subequal in length to tegmen, narrow, as in Figure 10.

Originally included species: Ennearthron (*Ceracis*) *sallei* Mellié (selected as type species above), *E.* (*C.*) *castaneipennis* Mellié, *E.* (*C.*) *militaris* Mellié, *E.* (*C.*) *furcifer* Mellié, *E.* (*C.*) *variabilis* Mellié.

Presently included species. As it is here delimited, the genus *Ceracis* includes a number of species formerly placed in *Ennearthron*, and several which have been removed from other genera. In the list below, the original generic placement and literature citation are given for each, as well as the type locality and location of type material where possible. Brief synonymies are given for all those species not treated later in the section on the North American fauna.

Ennearthron bicornis Mellié, 1848: 374. "Perou." Melly Coll., GEN.

Ennearthron californicum Casey, 1884: 36.

Ennearthron (*Ceracis*) *castaneipennis* Mellié, 1848: 376. "Cuba." Marseul Coll., MNHN.

Cis nitidulus Mellié, 1848: 334. "Lombardie." Marseul Coll., MNHN.

Ceracis ater Pic, 1922: 2. "Guadeloupe." Pic Coll., MNHN. NEW SYNONYMY.

Ceracis rufipes Pic, 1922: 2. "Guadeloupe." Pic Coll., MNHN. NEW SYNONYMY.

Ennearthron corniferum Mellié, 1848: 371. "Bresil." Marseul Coll., MNHN.

Ennearthron cucullatum Mellié, 1848: 372. "Cayenne." Pic Coll., (Chevrolat Coll.), MNHN.

Ennearthron tabelliferum Mellié, 1848: 373. "Cap de Bonne Esperance." Marseul Coll., MNHN. NEW SYNONYMY.

Ennearthron bilamellatum Pic, 1916a: 20. "Madagascar." Pic Coll., MNHN. NEW SYNONYMY.

Ennearthron lamellatum Pic, 1939: 8. "Bresil." Pic Coll., MNHN. NEW SYNONYMY.

Ennearthron curtum Mellié, 1848: 367.

Ennearthron cylindricum Brethes, 1922: 303. "General Urquiza." [Argentina]. Location of type unknown.

Octotemnus dixiensis Tanner, 1934: 47.

Scoltyocis evansi Blair, 1944: 126. "Fiji: Taveuni." BMNH.

Bostrichus furcatus Bosc, 1791: 6. "Jamaica." Location of type unknown.

Ennearthron (*Ceracis*) *furcifer* Mellié, 1848: 379. "Cayenne." Melly Coll., GEN.

Ceracis semipallidus Pic, 1922: 3. "Guadeloupe." Pic Coll., MNHN. NEW SYNONYMY.

Cis furcicollis Blair, 1935: 295. "Hiva Oa: Kopaafaa." [Marquesas]. BBM.

Ennearthron hastiferum Mellié, 1848: 370. "Colombie." Melly Coll., GEN.

Ennearthron japonum Reitter, 1878: 36. "Japan." Pic Coll. (Reitter Coll.), MNHN.

Xylographus latirostris Gorham, 1886: 355. "Guatemala. . . .Zapote." BMNH.

Ennearthron (*Ceracis*) *militaris* Mellié, 1848: 378. "Mexique." Marsuel Coll., MNHN.

Cis minutissimus Mellié, 1848: 334.

Ceracis minuta Dury, 1917: 25.

Ceracis monocerus, NEW NAME (See below).

Ennearthron multipunctatum Mellié, 1848: 368.

Ennearthron nigricans Fauvel, 1904: 163. "Noumea." [New Caledonia]. Fauvel Coll., BRUS.

Ceracis nigropunctatus, NEW SPECIES (See below).

Ceracis obrieni, NEW SPECIES (See below).

Ceracis palaceps Zimmerman, 1942: 51. "Guam." USNM.

Ceracis powelli, NEW SPECIES (See below).

Ennearthron pullulum Casey, 1898: 90.

Ceracis punctulata Casey, 1898: 90.

Ceracis punctulatus rubriculus, NEW SUBSPECIES (See below).

Ceracis quadricornis Gorham, 1886: 359.

Ceracis quadridentatus Pic, 1922: 3. "Guadeloupe." Pic Coll., MNHN.

Ceracis ruficornis Pic, 1916a: 20. "Bresil." Pic Coll., MNHN.

Ennearthron (*Ceracis*) *sallei* Mellié, 1848: 377.

Ceracis schaefferi Dury, 1917: 25.

Ennearthron shikokuense Miyatake, 1954: 56. "Omogokei, Iyo." [Shikoku, Japan]. Matsuyama Agric. College, Japan.

Ennearthron simplicicorne Pic, 1916a: 19. "Buenos-Ayres." Pic Coll., MNHN.

Ceracis similis Horn, 1894: 391. "Coral de Piedra, Sierra el Taste." [Baja California]. CAS.
Xestocis singularis Dury, 1917: 15.
Ennearthron taurulus Jacquelin DuVal, 1857: 245. "Cuba." Guerin-Meneville Coll., BRUS.
Ceracis bison Reitter, 1878: 37. "Cuba." Oberthur Coll., MNHN. NEW SYNONYMY.
Cis thoracicornis Ziegler, 1845: 270.
Ceracis unicornis Gorham, 1898: 332. "St. Vincent." [West Indies]. BMNH.
Ennearthron (*Ceracis*) *variabilis* Mellié, 1848: 380. "Cuba." Pic Coll. (Chevrolat Coll.), MNHN.

Five other species described in this genus have been or are here removed. *Ceracis compressicornis* Fairmaire was placed in the genus *Cis* by Lesne (1917); it belongs to a group of Indo-Pacific species, which are short and broad, and have a carinate prosternum, expanded (but not spinose) protibial apex, and 2 long, frontoclypeal horns in the male. *Ceracis tricornis* Gorham (1883: 224) and *Ceracis sumatrensis* Pic (1916b: 6) both should be placed in the genus *Cis*. The two species have a carinate prosternum, 10-segmented antennae, and a dentate protibial apex, and they would be placed within the genus *Eridaulus*, as delimited by me in a recent publication (Lawrence, 1965: 282). A further study of this group, however, has raised some doubt in my mind as to the distinctness and homogeneity of *Eridaulus*. *Ceracis tricornis* belongs to the *Xestocis miles* complex, while *C. sumatrensis* is related to *Cis pacificus* and its allies; these two species groups are distinct from the *Cis nitidus* group (*Eridaulus*) and all three probably should be included within the genus *Cis*. *Ceracis bifurcus* Gorham (1898: 332) and *Ceracis laticornis* Pic (1922: 3) have 10-segmented antennae, carinate prosternum, and a protibia which is serrate along the outer edge, while *Ceracis particularis* Pic (1922: 3) has 8-segmented antennae, a broad prosternal intercoxal process, and rounded protibial apex; these three species cannot be placed in any existing genus.

Etymology. Keras, Gr., horn + kis, kios, Gr., woodboring worm or weevil; masculine.

Distribution. Widespread and common in the New World, from southern Canada to Argentina, with 34 described species. Also known from South Africa, Madagascar and vicinity (1 species), Japan (2 species), Micronesia (1 species), Polynesia (2 species), and New Caledonia (1 species). Only one introduced species (*C. cucullatus*) known in the European fauna. A large number of Neotropical species and several Indo-Pacific species remain to be described.

Host range. Since little or nothing is known about the biology of many species, it is difficult to generalize about host range at the generic level. A few general remarks can be made at this point and a more detailed discussion of host preferences will be included in the section on North American species. All of the species of *Ceracis* for which biological data have been recorded occur on the woody fungi (especially Polyporaceae), in contrast to the members of the genus *Orthocis* and a number of *Cis*, which are associated with softer fruiting bodies or mycelial growth. Since the genus is primarily a tropical one, many species have been collected in the fruiting bodies of *Ganoderma*, a large genus of polypores with many tropical forms. A number of New World species occur on a group of fungi which have reddish or brownish sporophores (*Polyporus gilvus* group), and in North America these are practically the only species which utilize these fungi. Members of the *Ceracis furcifer* group (discussed below) appear to be restricted to *Polyporus versicolor* and its relatives. Some of the species of *Ceracis* occur on a large number of different fungi, but several others appear to be rather host specific.

Discussion. Although the members of the genus *Ceracis* can be easily distinguished from species of *Cis* and most other Ciinae by the concave prosternum, laminate prosternal process, and spinose protibial apex, there are several other described genera which have one or more of these characters. The genera *Strigocis* Dury and *Sulcacis* Dury have a similar protibial struc-

ture; in *Sulcacis* the prosternum is somewhat concave or biconcave, but the intercoxal process is broader, while in *Strigocis* the prosternum is strongly tumid and carinate, the anterior pronotal angles are more pronounced, and the elytral suture is margined posteriorly. In both genera, the vestiture consists of longer hairs or stout bristles, and aedeagus is of a different type. *Falsocis* Pic and *Neoennearthron* Miyatake have a similar prosternum with the intercoxal process laminate, but both have a different protibial structure. The two closely related and probably synonymous genera *Wagaicis* Lohse and *Odontocis* Nakane and Nobuchi resemble *Ceracis* with respect to the prosternal structure, protibial structure, and type of vestiture, but in both genera the anterior angles are somewhat produced and the aedeagus is of a different type. In *Paraxestocis* Miyatake, the intercoxal process is laminate and the protibia is spinose, but the prosternum is carinate and the protibial spines extend proximad along the outer edge. *Malacocis* Gorham is also characterized by having a concave prosternum, laminate intercoxal process and spinose protibial apex, but the members of this genus are very short and broad, with a very short prosternum, and the vestiture consists of short, stout bristles.

Notes on species and species groups. Although the main body of this paper is devoted to the North American representatives of *Ceracis*, the following section has been included to clarify some of the relationships among the species not occurring north of Mexico or found only in the Old World. Some of the more apparent species synonymies have been included in the species list above, but a few other names will probably be placed in synonymy when a more thorough study of the genus is undertaken.

Ceracis furcifer group. This group consists of 9 described New World species, one of which (*C. semipallidus* Pic) has been synonymized with *C. furcifer*. All of the species have a similar body form, fine and sparse pronotal and elytral punctation, a rounded or shallowly emarginate pronotal apex and a median frontoclypeal horn in the male. Six of these species—*C. cornifer*, *C. cylindricus*, *C. hastifer*, *C. monocerus*, *C. simplicicornis*, and *C. unicornis*—have 9-segmented antennae, and a frontoclypeal horn which is rounded, truncate, or shallowly emarginate at the apex. The other two species—*C. furcifer* and *C. ruficornis*—have 8-segmented antennae and a frontoclypeal horn which is deeply incised at apex so that 2 branches are formed. The species within each subgroup differ only in characters of color, punctation, and horn shape, and most of them are allopatric on the basis of known material. These described forms may well be races of 2 polytypic species, but they have not been considered as such, either because the type has not been examined (*C. cylindricus*) or because sufficient series are not yet available.

Ceracis cucullatus group. This group consists of at least 5 species—*C. cucullatus*, *C. bicornis*, *C. tabellifer*, *C. bilamellatus*, and *C. lamellatus*—the last 3 of which have been synonymized with *C. cucullatus* above. The North American *C. thoracicornis* may also be included in this group. The species are moderately long and narrow, with 9-segmented antennae, fine and sparse pronotal and elytral punctation, and a relatively long lamina on the pronotal apex of the male, this lamina being deeply emarginate in *C. bicornis* (and in *C. thoracicornis*) so that 2 narrow horns are formed, but very shallowly emarginate in *C. cucullatus*. The other 3 forms were described as new on the basis of size and development of pronotal characters in the male, both of which vary within any one population. *C. cucullatus* is the most widespread species in the family. It is common throughout the Neotropical region from central Mexico to southern Brazil; Scott (1926) has reported it from Grenada, and I have seen a large number of specimens from the Galapagos Islands. In the Old World, it has been recorded from France (noted as an intro-

duction), South Africa, N. W. Rhodesia, Madagascar, Reunion, Mauritius, the Seychelles, and Aldabra (Abeille de Perrin, 1874; Lesne, 1917; Mellié, 1848; and Scott, 1926). The Old World specimens do not appear to be specifically distinct from the Neotropical form, and the present range in southern Africa and the Malagasy region is probably the result of a recent expansion following an early introduction from South America. *C. bicornis* is also widespread in the New World tropics, and specimens have been seen from Mexico, Guatemala, Cocos Islands, Costa Rica, Peru, and southern Brazil.

Ceracis furcatus, C. variabilis, C. militaris, and *C. minutus*. These 4 names apply to very small species, which may or may not be related, but which are easily confused and have been erroneously cited in the literature. *C. furcatus* (Bosc) is known only from a short description and a figure (Bosc, 1792: 259, pl. 38, A–C); Lesne (1917) placed it in the genus *Ceracis* on the basis of the illustration. The diverging pronotal horns are very similar to those in Mellié's figure of *C. militaris*, but the type specimen of *C. militaris* does not look like the same species. Gorham (1883) synonymized *C. furcifer* (discussed above) with *C. militaris*, on the basis of misidentified specimens in the Sallé collection, and recorded the species from several localities in Mexico and Guatemala. In 1886, he noted his error and referred all but one series of specimens to *C. furcifer*. The remaining series from Veracruz was identified as *C. militaris*, but I have not seen the specimens to verify this. In 1898, Gorham referred a series from St. Vincent to *militaris* as well. *C. variabilis* was described by Mellié on the basis of Cuban specimens with 2 very weak tubercles on the pronotal apex of the male. After examining the collections in Paris, I could find only a single female which may have come from the type series of Mellié; in general form and punctation, this specimen appears to be conspecific with a series from Antigua, Puerto Rico, Cuba, Montserrat, and the Virgin Islands, the larger males of which have horns resembling Bosc's illustration of *C. furcatus*. I think that *C. variabilis* is probably synonymous with the Jamaican *C. furcatus* and with Gorham's "*militaris*" from St. Vincent, and that *C. militaris* from Mexico is a distinct species. *C. minutus*, from North America and the West Indies, is probably related to this group, but it appears to be a distinct species. Further collecting in Mexico will be necessary to clarify the status of *C. militaris*.

"*Xylographus*" *latirostris*. This species was described from a pair of specimens from Zapote, Guatemala. The male holotype has 10-segmented antennae and a rather stocky appearance like that of *Xylographus*, but several characters exclude it from that genus. The procoxae, intercoxal process, and protibial apex are of the *Ceracis* type, and I think the species should be placed provisionally in this genus. The "female" paratype is actually a male of an entirely different species, and it belongs in a genus which is not yet described.

Miscellaneous Neotropical species. *Ceracis castaneipennis* is widespread in the West Indies but does not extend into the United States. It is probably related to *C. curtus* and is further mentioned in the discussion of the latter species. *Ceracis quadridentatus* is known from only 2 specimens collected on Guadeloupe. It is apparently a distinct species, but sufficient notes were not taken on the type to relate it to other Neotropical *Ceracis*. *Enneathron taurulus* from Cuba is a short and broad species with 2 long frontoclypeal horns in the male; it does not appear to be closely related to any other *Ceracis*.

Indo-Pacific *Ceracis*. *Enneathron japonum* and *E. shikokuense* are two closely related species from Japan; both are elongate and have 9-segmented antennae. The two species may form part of the *Ceracis cucullatus* group. *C. furcicollis* was placed by Blair in the genus *Cis* because of the 10-

segmented antennae; it definitely belongs in *Ceracis* and closely resembles *C. singularis* in the form of the pronotal horns. *Scolytocis evansi* is a peculiar species with a single horn on the pronotum and another erect horn on the vertex in the male; Blair described this species at a time when the type of *Scolytocis samoensis* was not available for comparison. *S. samoensis* is the only described species in that genus, which is related to *Xylographus*. *Ceracis palaceps* from Micronesia and *Ennearthron nigricans* from New Caledonia are both distinct species of *Ceracis* which are probably not closely related to any other known form.

THE NORTH AMERICAN SPECIES OF *CERACIS*

Ceracis is the second largest genus of Ciidae occurring in the New World, consisting of 35 described forms distributed from southern Canada to Argentina. In North America, there are 18 species, 4 of which are here described as new. In the present treatment, species which occur in Mexico but do not extend into the United States are excluded. The present revision must be considered as a preliminary one, since there are several undescribed species in the southeastern United States, for which adequate series are not yet available.

Origin and distribution. The North American species of *Ceracis* appear to be entirely Neotropical in origin. With the exception of two species in southern Japan, there are no *Ceracis* in the Palaearctic region and the several Indo-Pacific species do not appear to be closely related to any of the New World forms. The group may have originally developed in the Old World, however, since several related genera (*Wagaicis*, *Odontocis*, *Neoennearthron*, and *Paraxestocis*) occur there. The genus is a dominant group in the New World and includes some of the commonest species in the North American fauna.

The species of *Ceracis* occurring in the United States and Canada may be placed in 4 groups on the basis of distributional patterns:

1) Northern Group. These species are fairly widely distributed throughout the eastern part of the continent and usually extend into the northern United States and southern Canada. With 2 exceptions (a single record each of *C. singularis* from Costa Rica and *C. punctulatus* from western Cuba) none of the species extend south of the United States. Included species: *C. minutissimus*, *C. punctulatus*, *C. sallei*, *C. singularis*, *C. thoracicornis*.

2) Western Mexican Group. These species occur in western Mexico and the southwestern United States, with one of them, *C. californicus*, extending north along the Pacific Coast. Included species: *C. californicus*, *C. dixiensis*, *C. obrieni*, *C. powelli*.

3) Eastern Mexican Group. The three species in this group occur along the Gulf Coast and extend into eastern Mexico and Central America. Included species: *C. nigropunctatus*, *C. quadricornis*, *C. schaefferi*.

4) West Indian Group. Members of this group occur in the Gulf Coast area and the Southern Coastal Plain, but are most common in Florida and the Greater Antilles. Included species: *C. curtus*, *C. minutus*, *C. monocerus*, *C. multipunctatus*, *C. pullulus*.

It is probable that the species in the first group include most of the older elements in the North American fauna, while those in the last three groups, with the possible exception of *C. californicus*, represent more recent southern derivatives.

Linsley (1958), in his analysis of North American cerambycid beetles, recognized five major faunas and one subfauna. The Holarctic and Vancouveran faunas include younger and older northern elements with Palaearctic affinities and cannot be applied to the species of *Ceracis*. The Alleghenian fauna consists of both northern and southern elements, which have entered the fauna early enough to exist as endemics in North America. The 5 species in group 1), above, probably correspond to the southern ele-

ments of Linsley's Alleghenian, and, like the cerambycids in this fauna, they are associated with the eastern lowland hardwood forests. The Neotropical fauna consists of relatively recent southern elements which occur in eastern North America and also in the West Indies or Mexico; the species in groups 3) and 4), above, represent elements of this fauna. Group 2) corresponds with Linsley's Sonoran fauna in the broad sense, since the species occur both in the Southwest and in northern Mexico. *Ceracis dixiensis* and probably *C. obrieni* are typical members of the Sonoran fauna and inhabit the Lower Sonoran Life Zone, but *C. californicus* and *C. powelli* usually occur in the Upper Sonoran and Transition zones. The distribution of *C. californicus* is more suggestive of the Californian subfauna, which consists of older southern elements.

Host preference. Although it may seem inappropriate to include a discussion of fungi and ecological preferences in a purely taxonomic paper, a brief treatment is included here to emphasize the role of host selection in the evolution of the Ciidae and to clarify the statements on host specificity in the species discussions to follow. A more general work on host preference in the North American Ciidae will soon be ready for publication, so that future taxonomic papers will not be similarly burdened.

The majority of species of Ciidae live the greater part of their lives within the dead fruiting bodies of various wood-rotting fungi (Basidiomycetes: Polyporaceae, Hydnaceae, Thelephoraceae, and Agaricaceae), where both larvae and adults feed on sterile hyphal tissue. This type of habitat differs from that formed by the ground-inhabiting fungi (Boletaceae and most Agaricaceae) in that the substrate is tougher and more durable, allowing the insects to complete their development within a single fruiting body and at the same time necessitating the development of boring adaptations similar to those evolved in various groups of xylophagous insects.

It has long been suspected that mycetophagous beetles exhibit a preference for one or more fungus species, and early workers, such as Weiss and West (1920, 1921), and Donisthorpe (1935), published lists of known host associations and emphasized the value of correct fungus identifications. In recent years, several papers have been published on the food habits of fungus beetles (Benick, 1952; Graves, 1960; Rehfous, 1955; Scheerpeltz and Höfler, 1948), but the first worker to clearly demonstrate the existence of host preference patterns in the Ciidae was Paviour-Smith (1960), in a study based on 10 ciid species occurring in southern England. Intensive field studies in Wytham Woods, near Oxford, England, and a critical compilation of previous host records for that general area revealed that the fungi could be placed into two distinct groups, each with a characteristic fauna of ciid beetles. The first group includes *Polyporus versicolor*, *P. hirsutus*, *Lenzites betulina*, and *Trametes gibbosa*, all of which have a complex (trimitic) hyphal system, while the second group includes a somewhat more diverse assemblage (*Polyporus betulinus*, *P. adustus*, *Ganoderma applanatum*, *Pleurotus sapidus*, and others) which are characterized by having a simpler (monomitic or dimitic) hyphal system. The beetles rarely occurred on fungi in the "wrong" group, and within each group particular beetle species often preferred a single fungus, which was termed its "headquarters." My own unpublished data on the North American Ciidae tend to support the existence of these two host preference groups based on hyphal structure, as well as two more groups including fungi which were not treated in Paviour-Smith's study. These will be mentioned below as they pertain to the species of *Ceracis*.

Before continuing with the subject of host preference, it is necessary to make a few remarks on the classification of the wood-rotting fungi. At the present time, the generic limits in the Polyporaceae and related families are controversial, and so many generic names have been proposed that some

authorities, including Lowe and Gilbertson, have utilized the older Friesian genera, which are admittedly based on superficial morphological characters of the sporophore and do not necessarily reflect current ideas on the evolution of the group. A clearer picture of the phylogenetic relationships among these fungi is gradually emerging as a result of studies on the microstructure of the fruiting body (Cunningham, 1947) and the characters of living cultures (Nobles, 1958, 1965; Lowe and Gilbertson, personal communication).

The following are the species of fungi from which various *Ceracis* have been recorded:

Boletaceae: *Boletus* sp. (the only ground-inhabiting fungus; a single record of *C. thoracicornis* is almost certainly accidental).

Agaricaceae: *Pleurotus ostreatus* Jacq.

Hydnaceae: *Steccherinum ochraceum* (Pers.) S. F. Gray.

Polyporaceae: *Ganoderma applanatum* (Pers. ex Wallr.) Pat., *G. brownii* (Murr.) Gilb., *G. lobatum* (Schw.) Atk., *G. lucidum* (Leys. ex Fries) Karst., *G. zonatum* Murr., *G. curtisii* Murr., *G. oregonense* Murr., *G. tsugae* Murr., *Ganoderma* spp. (several unidentified species).

Fomes robiniae (Murr.) Sacc. & Sacc., *F. conchatus* (Pers. ex Fries) Gill., *F. igniarius* (L. ex Fries) Kickx, *F. fomentarius* (L. ex Fries) Kickx, *F. sclerodermeus* (Lev.) Cooke, *F. cajanderi* Karst., *F. fraxinophilus* (Peck) Cooke, *F. pinicola* (Swartz ex Fries) Cooke, *F. annosus* (Fries) Karst.

Daedalea unicolor Bull. ex Fries, *D. ambigua* Berk.

Lenzites betulina (L. ex Fries) Fries, *L. striata* (Swartz ex Fries) Fries, *L. saepiaria* (Wulf. ex Fries) Fries.

Trametes mollis (Sommerf.) Fries, *T. hispida* Bagl., *T. corrugata* (Pers.) Bres.

Poria versipora (Pers.) Rom., *P. nigra* (Berk.) Cooke.

Polyporus squamosus Mich. ex Fries, *P. sanguineus* L. ex Fries, *P. sulphureus* Bull. ex Fries, *P. adustus* Willd. ex Fries, *P. fumosus* Pers. ex Fries, *P. supinus* Swartz ex Fries, *P. abietinus* Dicks. ex Fries, *P. pargamenus* Fries, *P. sector* Ehrenb. ex Fries, *P. versicolor* L. ex Fries, *P. maximus* (Mont.) Overh., *P. hirsutus* Wulf. ex Fries, *P. occidentalis* Klotz., *P. spraguei* Berk. & Curt., *P. iodinus* Mont., *P. gilvus* (Schw.) Fries, *P. licnoides* Mont., *P. radiatus* Sow. ex Fries, *P. hydnoides* Swartz ex Fries.

The genus *Ganoderma* is a natural grouping of fairly closely related forms, but many tropical and subtropical species are very difficult to identify; for this reason records of unidentified *Ganoderma* have been included in the host data. Some authorities consider *G. brownii* and *G. zonatum* to be varieties of *G. applanatum* and *G. lucidum* respectively. All of the other genera appear to be heterogeneous assemblages, and records from "*Polyporus* sp." or "*Fomes* sp." have been disregarded. *Fomes robiniae*, *F. conchatus*, and *F. igniarius* are similar in having brownish sporophores (and mycelial mats), and Nobles (1958) has grouped them together with brownish species of *Polyporus*, such as *P. gilvus*, *P. iodinus*, and *P. licnoides*. *Fomes fomentarius* and *F. sclerodermeus* are very closely related species occurring in the northern and southern states, respectively. *Polyporus versicolor*, *P. hirsutus*, *P. occidentalis*, and *P. maximus* are similar in having relatively thin, whitish sporophores with a trimitic hyphal system, and on the basis of cultural and other characters they are thought to be related to *Lenzites betulina*, *Trametes hispida*, and *Daedalea ambigua*. *Polyporus pargamenus* and its close relatives *P. sector* and *P. abietinus* are also thought to belong to the *P. versicolor* group, but they appear to be preferred by different ciids.

The following outline of host preference groups must be tentative, since it involves only the 17 species of North American *Ceracis*, but it is, for the most part, supported by unpublished data for over 100 species of Nearctic and Neotropical Ciidae.

Polyporus versicolor group. This is essentially the same as the group proposed by Paviour-Smith (1960) with the addition

of a few American species. The only two species of *Ceracis* which definitely prefer this group of fungi are *C. dixiensis*, which is normally found on *Trametes hispida*, and *C. quadricornis*, which occurs on several species, including *P. occidentalis* and *P. hirsutus*. *C. thoracicornis* and *C. californicus* both occur regularly on fungi in this group, but both are rather polyphagous and probably have their "headquarters" in other groups (see below). *C. monocerus* has been taken only on *Polyporus sanguineus*. This fungus differs from *P. versicolor* and its relatives in the shape of the basidiospore and the bright reddish color of the fruiting body, but it would fall into this group on the basis of the hyphal system (Cunningham, 1947) and host records for several Neotropical ciids.

Polyporus pargamenus group. This includes *P. pargamenus*, *P. abietinus*, *P. sector*, and probably *Daedalea unicolor*, all of which have relatively thin sporophores with whitish context and violet to gray or brownish pore surface. The 3 *Ceracis* which seem to prefer these fungi are *C. thoracicornis*, *C. minutissimus*, and *C. powelli*. Although *C. thoracicornis* occurs on a wide variety of hosts, it shows a definite preference for *P. pargamenus* and is a common and characteristic inhabitant of the other species as well. *C. powelli* has been taken only on *P. abietinus* and *P. pargamenus*, while *C. minutissimus* occurs only on *D. unicolor*.

Polyporus gilvus group. A number of fungi with brownish or reddish brown fruiting bodies are included here. Some of these are *Polyporus gilvus*, *P. lienoides*, *Poria nigra*, *Fomes robiniae*, and *F. igniarius*. The 4 species definitely preferring fungi in this group are *C. singularis*, *C. obrieni*, *C. punctulatus*, and *C. pullulus*. Some of these beetles also breed in *Polyporus hydnoides* and certain *Ganoderma*, which have brownish sporophores, but which are usually inhabited by a different group of beetles (see below).

Ganoderma applanatum group. This corresponds to Paviour-Smith's second host preference group, characterized by the dimitic or monomitic hyphal system, and includes most of the remaining fungi, for which there are adequate host records. The beetles included are: *Ceracis sallei*, *C. schaefferi*, *C. minutus*, *C. multipunctatus*, *C. nigropunctatus*, *C. curtus*, and *C. californicus*. *C. sallei* occurs almost exclusively on *Ganoderma applanatum*, while *C. multipunctatus* is usually found on *G. zonatum*. *C. nigropunctatus* and *C. curtus* both occur on *Fomes sclerodermeus* and *Polyporus hydnoides*. *C. minutus* and *C. schaefferi* are doubtfully included on the basis of a single record on *Ganoderma*. *C. californicus* is another species with a wider host range, but it appears to prefer the species of *Ganoderma* as well as *Polyporus adustus*, which also falls into this group.

The placing of fungi and beetles into distinct groups is obviously an oversimplification, but it does serve to bring to light certain patterns of host preference. There are probably several characteristics of the fungus sporophore which are involved in host selection, two of these being chemical composition (as reflected in the color) and texture (which is probably connected with the complexity of the hyphal system). Some beetle species will be less host specific than others and may occur on fungi in several groups. A satisfactory analysis of host preference phenomena must take into account several other factors, such as the condition of fruiting bodies (wet or dry, fresh or decomposed), host range and relative abundance of the fungi, geographic distribution of the fungi and the beetles, and the presence of closely related or competing beetle species in any particular area. Some of these will be considered in the discussions of individual species.

Key to the Species of *Ceracis* Occurring in in North America

Males

1 Apex of pronotum rounded or weakly emarginate, without distinct tubercles, horns, or lamina ..... 2)

— Apex of pronotum produced, forming a lamina, or 2 tubercles or horns ..... 6)

2) Frontoclypeal ridge produced, forming a long and narrow, median horn; pronotal and elytral punctation very fine and sparse ..... *C. monocerus*, new name

— Frontoclypeal ridge simple, or forming 2 rounded plates or tubercles; elytral punctation much coarser and denser than pronotal punctation ..... 3)

3) Abdominal pore transverse, and at least 0.50 × as long as body of sternite III .. 4)

— Abdominal pore circular, and less than 0.40 × as long as body of sternite III .. 5)

4) Size larger, TL more than 1.40 mm; frontoclypeal ridge simple; pronotal disc strongly declined anteriorly, the apex rounded; elytra expanded near apices ..... *C. obrieni*, n. sp.

— Size smaller, TL less than 1.40 mm; frontoclypeal ridge forming 2 tubercles; pronotal disc only weakly declined anteriorly, the apex shallowly emarginate; elytra subparallel .... *C. dixiensis* (Tanner)

5) Body longer and narrower, EL/EW more than 1.45; EL/PL more than 1.85; pronotal apex very shallowly emarginate; elytral punctation dual and confused; southern Arizona ..... *C. powelli*, n. sp.

— Body shorter and broader, EL/EW less than 1.45; EL/PL less than 1.85; pronotal apex rounded; elytral punctation single and uniform; Florida ..... *C. multipunctatus* (Mellié)

6) Elytral punctation distinctly seriate; antennae 9- or 10-segmented 7)

— Elytral punctation not distinctly seriate; if subseriate, then antennae 8-segmented ..... 8)

7) Antennae 10-segmented; pronotal apex bearing 2 horns, each with a distinct knob above; abdominal pore slightly transverse ..... *C. singularis* (Dury)

— Antennae 9-segmented; pronotal apex with 2 flattened horns; abdominal pore circular ..... *C. pullulus* (Casey)

8) Elytral punctation single and uniform, very coarse and dense; body shorter and broader, EL/EW less than 1.35; antennae 9-segmented ..... 9)

— Elytral punctation distinctly dual, the punctures usually falling into 2 size classes; if obscurely dual, then EL/EW more than 1.35 or antennae 8-segmented ..... 10)

9) Size larger, TL usually more than 1.50 mm; sides of elytra somewhat rounded; body somewhat shorter and broader; surfaces of pronotum and elytra smooth *C. curtus* (Mellié)

— Size smaller, TL usually less than 1.50 mm; sides of elytra subparallel; body somewhat longer and narrower; surfaces of pronotum and elytra lightly granulate ..... *C. nigropunctatus*, n. sp.

10) Antennae 9-segmented ..... 11)

— Antennae 8-segmented ..... 12)

11) Apex of pronotum with a deeply emarginate lamina or 2 flattened, subtriangular horns; elytral punctation coarser and denser, the punctures usually separated by less than 0.75 diameter; western North America .. *C. californicus* (Casey)

— Apex of pronotum with 2 distinctly tumid, narrow, diverging horns; elytral punctation finer and sparser, the punctures usually separated by 0.75 diameter or more; eastern North America ..... *C. thoracicornis* (Ziegler)

12) Body longer and narrower, TL/EW more than 2.40; apex of pronotum with 2 narrow, diverging horns ..... *C. quadricornis* Gorham

— Body shorter and broader, TL/EW less than 2.40; apex of pronotum with a short, broad lamina or 2 flattened, subtriangular horns or teeth ..... 13)

13) Elytral punctation much coarser and denser than pronotal punctation ..... 14)

— Elytral punctation as fine and sparse as or finer and sparser than pronotal punctation ..... 15)

14) Size larger, TL usually more than 1.30 mm; EL/PL usually less than 1.60; pronotal punctation somewhat coarser and denser, the punctures usually more than 0.10 × as large as scutellar base and separated by 1.5 diameters or less; pronotal apex with a short, broad, elevated lamina; color usually uniformly reddish, southern Texas ..... *C. schaefferi* Dury

— Size smaller, TL usually less than 1.30 mm; EL/PL usually more than 1.60; pronotal punctation somewhat finer and sparser, the punctures usually less than 0.10 × as large as scutellar base and separated by more than 1.5 diameters; pronotal apex with 2 approximate, triangular teeth; color blackish or dark brown, with pronotal apex yellowish; eastern North America ..... *C. minutissimus* (Mellié)

15) Size smaller, TL less than 1.5 mm; abdominal pore less than 0.33 × as long as body of sternite III; pronotal apex with 2 subparallel or slightly diverging, narrow horns; elytral punctation subseriate ..... *C. minutus* Dury

— Size larger, TL more than 1.5 mm; abdominal pore less than 0.33 × as long as body of sternite III; pronotal apex with a deeply emarginate lamina, giving the appearance of 2 broad, subtriangular horns; elytral punctation confused ..... 16)

16) Pronotal punctation as fine and sparse as elytral punctation, the punctures usually separated by 1 diameter or more; abdominal pore slightly transverse ..... *C. sallei* Mellié

— Pronotal punctation somewhat coarser and denser than elytral punctation, the punctures usually separated by less than 1 diameter; abdominal pore circular ..... 17)

17) Color of elytra uniformly blackish; Florida only ..... *C. punctulatus punctulatus* Casey

— Elytra reddish posteriorly; eastern North America ..... *C. punctulatus rubriculus*, n. ssp.

FEMALES

1) Elytral punctation dual and distinctly seriate, the larger punctures forming relatively straight rows; antennae 9- or 10-segmented ..... 2)

— Elytral punctation not distinctly seriate; if subseriate, then antennae 8-segmented ..... 3)

2) Antennae 10-segmented; size larger, TL usually more than 1.47 mm ..... *C. singularis* (Dury)

— Antennae 9-segmented; size smaller, TL usually less than 1.47 mm ..... *C. pullulus* (Casey)

3) Elytral punctation single and uniform, very coarse and dense; antennae 9-segmented; EL EW less than 1.40 ..... 4)

Elytral punctation distinctly dual, the punctures falling into 2 size classes; if obscurely dual, then antennae 8-segmented or EL EW more than 1.40 ..... 6)

4) Pronotal punctation finer and sparser, the punctures less than 0.10 × as large as scutellar base and separated by more than 0.75 diameter; pronotal disc strongly declined anteriorly, its surface distinctly granulate and dull, in contrast to the smooth and shiny elytral surface ..... *C. multipunctatus* Mellié

— Pronotal punctation coarser and denser, the punctures more than 0.10 × as large as scutellar base and separated by less than 0.75 diameter; pronotal disc not or weakly declined anteriorly, its surface similar in texture to that of elytra ..... 5)

5) Size larger, TL usually more than 1.55 mm; sides of elytra somewhat rounded; pronotum shorter and broader, PL/PW usually less than 0.88; surfaces of pronotum and elytra smooth ..... *C. curtus* (Mellié)

— Size smaller, TL usually less than 1.55 mm; sides of elytra subparallel; pronotum longer and narrower, PL/PW usually more than 0.88; surfaces of pronotum and elytra lightly granulate ..... *C. nigropunctatus*, n. sp.

6) Antennae 9-segmented ..... 7)

— Antennae 8-segmented ..... 10)

7) Elytral punctation finer and sparser, the punctures separated by more than 1 diameter; eastern North America ..... 8)

— Elytral punctation coarser and denser, the punctures usually separated by less than 1 diameter; western North America ..... 9)

8) Pronotal punctation very fine and sparse, the punctures less than 0.10 × as large as scutellar base and separated by 1.5 diameters or more; pronotum somewhat shorter and broader, PL/PW usually less than 0.91; metasternal suture more than 0.20 × as long as median length of metasternum; pronotum usually lighter in color than elytra ..... *C. monocerus*, new name

— Pronotal punctation coarser and denser, the punctures more than 0.10 × as large as scutellar base and separated by 1.5 diameters or less; pronotum somewhat longer and narrower, PL/PW usually more than 0.91; metasternal suture less than 0.25 × as long as median length of metasternum; elytra and pronotum usually similar in color ..... *C. thoracicornis* (Ziegler)

9) Pronotum distinctly narrowed anteriorly; EL PL more than 1.85; antennal segment III 2.00 × as long as IV ..... *C. powelli*, n. sp.

— Pronotum not distinctly narrowed anteriorly; EL PL less than 1.85; antennal segment III 3.00 × as long as IV ..... *C. californicus* (Casey)

10) EL PL less than 1.60 and elytral punctation much coarser and denser than pronotal punctation; southern Texas ..... *C. schaefferi* Dury

— EL PL more than 1.60 or elytral punctation not coarser and denser than pronotal punctation ..... 11)

11) Pronotal disc strongly declined anteriorly; elytra distinctly expanded near apices; southern Arizona ..... *C. obrieni*, n. sp.

— Pronotal disc not or only weakly declined; elytra not expanded near apices ..... 12)

12) TL/EW more than 2.35; elytral punctures separated by 0.75 diameter or more, not subconfluent anteriorly; southern Texas ..... *C. quadricornis* Gorham

— TL/EW less than 2.35 or elytral punctures separated by less than 0.75 diameter and becoming subconfluent anteriorly ..... 13)

13) Elytral punctation coarser and denser than pronotal punctation, the punctures becoming subconfluent anteriorly ..... 14)

— Elytral punctation finer and sparser than or as fine and sparse as pronotal punctation, the punctures not subconfluent anteriorly ..... 15)

14) Pronotum somewhat shorter and broader, PL/PW usually less than 0.90; antennal segment III 1.50 × as long as IV; eastern North America ..... *C. minutissimus* (Mellié)

— Pronotum somewhat longer and narrower, PL/PW usually more than 0.90; antennal segment III 2.00 × as long as IV; western North America ..... *C. dixiensis* (Tanner)

15) Size smaller, TL less than 1.10 mm; elytral punctation subseriate; pronotal surface lightly granulate and shiny ..... *C. minutus* Dury

— Size larger, TL usually more than 1.10 mm; elytral punctation confused; pronotal surface distinctly granulate and dull ..... 16)

16) Pronotal punctation about as fine and sparse as elytral punctation, the punctures usually separated by 1 diameter or more ..... *C. sallei* Mellié

— Pronotal punctation coarser and denser than elytral punctation, the punctures usually separated by less than 1 diameter ..... 17)

17) Elytra uniformly black; Florida ..... *C. punctulatus punctulatus* Casey

— Elytra reddish posteriorly; eastern North America .. *C. punctulatus rubriculus*, n. ssp.

Ceracis californicus (Casey), NEW COMBINATION

Fig. 15

Ennearthron californicum Casey, 1884: 36; Casey, 1898: 89; Dury, 1917: 24; Hatch, 1962: 234, pl. 48, fig. 7. Type locality: "California." Holotype, ♂, Casey Coll., USNM.

Ennearthron convergens Casey, 1898: 89; Dury, 1917: 24. Type locality: "California (Los Angeles)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Ennearthron discolor Casey, 1898: 89; Dury, 1917: 24. Type locality: "California (Sonoma Co.)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Ennearthron grossulum Casey, 1898: 89; Dury, 1917: 24. Type locality: "California (southern)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Ennearthron coloradense Dury, 1917: 22, 24. Type locality: "Grand Lake, Middle Park, Colo." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.

Ennearthron oregonus Dury, 1917: 22, 24; Hatch, 1962: 235 (syn.). Type locality: "Corvallis, Oregon." Holotype, ♂, Dury Coll. CIN.

Plesiotypes.— ♂ and ♀, CALIFORNIA: Alpine Lake, Marin Co., Jan. 30, 1960, Lot 523 J. F. Lawrence, ex *Ganoderma brownii* on *Umbellularia californica* [MCZ].

Male.—Length 1.80 mm. Body 2.57 × as long as broad. Head and apex or pronotum reddish, remainder of pronotum dark reddish brown; greater part of elytra blackish, posterior third reddish mesially; ventral surfaces blackish; legs and antennal club yellowish brown, antennal funicle and palpi yellowish. Vertex with a deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a relatively long, slightly concave lamina, which is shallowly emarginate at apex. Antennae 9-segmented; segment III 3 × as long as IV. Pronotum 1.07 × as long as broad, widest at anterior third; sides sub-parallel; anterior edge produced, forming a flat, slightly elevated lamina, which is deeply emarginate, giving the appearance of 2 slightly divergent, subtriangular horns; disc impressed anteriorly just behind lamina and bearing a short, transverse carina on each side of it; surface distinctly granulate;

punctures about 0.16 × as large as scutellar base and separated by 0.25 to 0.75 diameter. Elytra 1.53 × as long as broad and 1.48 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; punctation dual and confused, coarser and denser than pronotal punctation, the punctures usually separated by 0.25 diameter. Metasternum 0.59 × long as wide; suture 0.15 × as long as median length of sternite. Abdomen 0.94 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.23 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.75 mm. Body 2.41 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.96 × as long as broad; anterior edge rounded. Elytra 1.55 × as long as broad and 1.80 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum reddish orange to black, usually reddish or dark reddish brown with the apex reddish, occasionally reddish mesially and darker laterally; elytra yellowish orange to black, usually reddish or blackish with some reddish posteriorly. Color varies considerably throughout range, and four major patterns are common: all black, all red or reddish brown, black with some reddish on the apex of pronotum and posterior part of elytra, and pronotum reddish with the elytra blackish or black and red. Although all types may be found within a single population, reddish specimens are more common in southern Arizona, while those from the California coast tend to be blackish. Anterior edge of pronotum in smaller males is weakly produced and shallowly emarginate, so that 2 small tubercles or teeth are formed. In larger specimens these are replaced by a distinct lamina, which may have converging, parallel, or slightly diverging sides and which is emarginate to varying degrees, so that 2 distinct teeth or horns are formed. Variation also occurs in the angle of elevation of the lamina and in the degree to which the pronotum is impressed behind it. The length of the plate varies from about 0.10 to 0.25 × the total length of the pronotum. The size and density of pronotal punctures and the granulation of the pronotal surface also exhibit a certain amount of variation. On the whole, northern California specimens tend to have a more distinctly granulate and dull pronotum with coarser and denser punctures than do individuals from southern Arizona. Size and dimensions vary as follows in a series of 14 ♂ ♂ and 13 ♀ ♀ from Alpine Lake, Marin Co., California (Lot 523): TLmm ♂ 1.44–1.80 (1.68 ± 0.029), ♀ 1.34–1.73 (1.57 ± 0.032); TL/EW ♂ 2.33–2.61 (2.50 ± 0.021), ♀ 2.31–2.56 (2.42 ± 0.019); PL PW ♂ 1.03–1.08 (1.05 ± 0.005), ♀ 0.96–1.04 (1.00 ± 0.008); EL/EW ♂ 1.37–1.57 (1.49 ± 0.015), ♀ 1.48–1.61 (1.52 ± 0.014); EL/PL ♂ 1.40–1.57 (1.48 ± 0.013), ♀ 1.59–1.80 (1.70 ± 0.019). Total size range in material examined: 1.20–2.06 mm.

Distribution.—Western North America, from Seattle, Washington, east to western Nebraska, south along the Pacific Coast to southern California and through the Great Basin and Rocky Mountains to southern Arizona and New Mexico; extending into Mexico as far south as Baja California del Sur and southern Sinaloa (see Fig. 29). About 1600 specimens have been examined from the following localities: **UNITED STATES**: ARIZONA: Carr Canyon (Huachuca Mts.), 15 mi. E Douglas, Graham Mt., Madera Canyon (Santa Rita Mts.), Miller Canyon (10 mi. W Hereford, Huachuca Mts.), 1 mi. N Nogales, 3 mi. S Patagonia, 4 mi. NE Patagonia, Sabino Canyon (Santa Catalina Mts.), San Francisco Peaks, Southwestern Research Station (5 mi. SW Portal), Rustler Park (8 mi. W Portal); CALIFORNIA: Alpine Lake, Alum Rock Park, Atascadero, Ben Lomond, Berkeley, Big Sur, 9 mi. W Brookdale, Calistoga, Carmel, Carson Ridge, 2 mi. SW Chew's Ridge, Claremont, 14 mi. S Clayton, 1 mi. SE Crystal Lake, Cordelia, Cow Creek (Stan-

islaus National Forest), 10 mi. N Descanso, Dorset Camp (Sequoia National Park), Escondido, Fallbrook, Fresno, Glen Ellen, 6 mi. SE Gorda, Green Valley, Kaweah, Korbel, Lagunitas, Lake Lagunitas, Long Beach, Los Gatos, 2 mi. SE Los Gatos, Los Angeles, Macama Creek, Markwest Springs, Mill Valley, 1.5 mi. N Mt. Laguna, Mt. Tamalpais, Mt. Wilson, Napa, North Hollywood, Oakland, Ojai, Palo Alto, Pasadena, 2 mi. N Piercy, 2 mi. N Placerville, Redwood Glen, 3 mi. N. Refugio Beach, S. P. Taylor State Park, San Diego, San Dimas Canyon, Santa Barbara, Santa Cruz Mts., Santa Monica, Siskiyou Co., 12 mi. W Skagg's Springs, 2 mi. E Sonora, 6 mi. E Stewart's Point, Stockton, 2 mi. E Sveadal, Taylorville, Tilden Park, Twain, Warner's, Wilmington; COLORADO: Denver, Middle Park, Newcastle, 10 mi. S Steamboat Springs; NEBRASKA: 15 mi. W Sydney; NEVADA: 8 mi. SE Lamoille (Ruby Mts.); NEW MEXICO: Silver City; OREGON: Wheatland, Corvallis; UTAH: Aspen Grove, 14 mi. SE Heber, Provo, Salt Lake City, Timpanogas. Utah Lake (east side); WASHINGTON: College Place, 3 mi. S College Place, 5 mi. W College Place, Kooskooskie, Seattle; **MEXICO**: BAJA CALIFORNIA DEL SUR: La Laguna (Sierra Laguna); DURANGO: 3 mi. W El Salto; SINALOA: 8 mi. W El Palmito [AMNH, ANSP, BYU, CAS, CDA, CIN, CIS, CU, INHS, JFL, JS, KU, MCZ, UAL, UAZ, UCD, USNM, UW]. A series of specimens from New Haven, Connecticut, and 3 specimens from Washington, D. C. have probably been mislabeled.

Host fungi.—Polyporus versicolor [27 (7)]; *Polyporus adustus* [11(2)]; *Ganoderma brownii* [8(5)]; *Ganoderma* sp. [6 (3)]; *Lenzites betulina* [6]; *Ganoderma applanatum* [3(2)]; *Trametes hispida* [3 (2)]; *Pleurotus ostreatus* [3(1)]; *Poria versipora* [2(2)]; *Steccherinum ochraceum* [2(1)]; *Polyporus gilvus* [2]; *Ganoderma lucidum* [1(1)]; *Ganoderma lobatum* [1 (1)]; *Polyporus pargamenus* [1(1)]; *Daedalea unicolor* [1(1)]; *Fomes annosus* [1 (1)]; *Fomes fraxinophilus* [1(1)]; *Ganoderma oregonense* [1]; *Fomes cajanderi* [1]; *Trametes mollis* [1].

Discussion.—This is a large, narrow, and elongate species, which does not appear to be closely related to any other known form. It is most similar to *C. powelli*, from which it differs by having coarser, denser, and more uniform elytral punctation, smoother elytral surface, longer 3rd antennal segment, and more pronounced secondary sexual characters in the male. It is also somewhat similar to *C. thoracicornis* from eastern North America, but that species is smaller, with finer and sparser elytral punctation and different pronotal characters in the male.

The considerable variation in color and secondary sexual characters in this species has led to the proposal of several names based on variants which may occur within a single population. Casey (1898) described 3 California species, *Ennearthron convergens*, *E. discolor*, and *E. grossulum*, which were based on minor differences in pronotal punctation and the nature of the pronotal lamina and all of which are synonymous with his earlier name *E. californicum* (Casey, 1884). Dury (1917) described 2 more species, *E. oregonus* from Oregon and *E. coloradense* from Colorado, which also fall within the range of variation of Casey's *californicum*. As noted above, there is a certain amount of geographic variation with respect to color, pronotal punctation, and surface texture, but I do not think this is sufficient to warrant the recognition of subspecies. Dury (1917) mentioned a subspecies from New Mexico, but did not propose a name for it; all of the other names proposed by Casey and Dury refer to variants of the typical northern and coastal form.

C. californicus is a common and widespread species in western North America and is one of the few members of this genus to become established in northern and montane regions, which are dominated by a Holarctic fauna. The species has a very

broad host range; it has been collected on 20 different fungi and apparently breeds in at least 14 of these, the most common hosts being *Polyporus versicolor*, *P. adustus*, and various species of *Ganoderma*. Although the above records suggest that *P. versicolor* is the preferred host, there is some evidence that *Ganoderma applanatum* and its relatives form the "headquarters" for this species. If the several closely related species of *Ganoderma* are taken together, the total number of breeding records exceeds that for *P. versicolor*. Most of the collections of *P. versicolor* were made in northern and coastal California, and there was a definite collecting bias in favor of this fungus, since it is inhabited by several different ciids. Finally, *Ceracis californicus* is more commonly collected on *Ganoderma* in southern Arizona, which probably is closer to the center of its range. If the species originated in northern Mexico, there may have originally been selection pressure in favor of oligophagous feeding habits, since a number of other *Ceracis* occur in this area. The species then spread northward along the Pacific Coast and into the Rocky Mountain Region, where the absence of related species allowed an expansion of the host range.

Whatever its original preferred host may have been, *Ceracis californicus* must be considered a polyphagous species, at least in the northern part of its range. It is interesting that the commonest host fungi fall into both of the host preference groups established by Paviour-Smith (1960) and corroborated by my own unpublished data on the North American ciids. *Polyporus versicolor* and *Lenzites betulina* form part of one group, and *Polyporus adustus* and *Ganoderma* spp. fall into the other. The same is true in the case of *Ceracis thoracicornis* discussed below.

In northern California, *C. californicus* is a common inhabitant of *Ganoderma brownii*, where it may occasionally be found with *Eridaulus ephippiatus* (Mannerheim). In the same area it is usually associated with *Sulcacis curtulus* (Casey) and *Eridaulus americanus* (Mannerheim) in *Polyporus adustus*, and it occurs with several other ciids, including *Cis vitulus* Mannerheim, *Cis versicolor* Casey, *Cis fuscipes* Mellié, and *Octotemnus laevis* Casey in *Polyporus versicolor* and its relatives. In Nevada and Utah, the species has been taken in *Ganoderma applanatum*. In southern Arizona and northern Mexico, it is usually found in various species of *Ganoderma*, including *G. lobatum* and *G. lucidum*, and it may occur in *Trametes hispida* as well. In this last area, there are 4 sympatric species of *Ceracis*, each of which occurs on a different group of fungi: *C. californicus* on *Ganoderma*, *C. dixiensis* on *Trametes hispida*, *C. powelli* on *Polyporus abietinus* and the related *P. pargamenus*, and *C. obrieni* on *Polyporus gilvus*.

Ceracis curtus (Mellié), NEW COMBINATION

Ennearthron curtum Mellié, 1848: 367, pl. 12, fig. 15; Jacquelin DuVal, 1857: 243. Type locality: "Havane." Lectotype, ♂, Pic Coll. (Chevrolat Coll.), MNHN.

Cis obesus Mellié, 1848: 335, pl. 11, fig. 13. Type locality: "Amerique boreale." Lectotype, ♂, Melly Coll., GEN. NEW SYNONYMY.

Ennearthron compacta Dury, 1917: 21, 24. Type locality: "Key West, Fla." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.

Plesiotypes.— ♂ and ♀, CUBA: Soledad (Cienfuegos), V, VI-'39, C. Parsons, coll. [MCZ].

Male.—Length 1.50 mm. Body 1.93 × as long as broad. Head and apex of pronotum reddish, remainder of pronotum black; elytra and ventral surfaces dark reddish brown; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with a weak, transverse impression, preceded by a median elevation; frontoclypeal ridge weakly produced and shallowly emarginate, forming 2 small, rounded tubercles. Antennae 9-segmented; segment III 2.25 × as long as IV. Pronotum 0.83 × as long as broad, widest at middle; sides

strongly rounded; anterior edge weakly produced and shallowly emarginate, forming 2 rounded, slightly elevated tubercles; surface very lightly granulate, almost smooth; punctures about 0.18 × as large as scutellar base and separated by 0.25 to 0.50 diameter. Elytra 1.16 × as long as broad and 1.50 × as long as pronotum; sides weakly rounded and slightly diverging for two-thirds of their lengths and abruptly converging at apices; punctation single and relatively uniform, coarser and somewhat denser than pronotal punctation, the punctures usually separated by 0.25 diameter. Metasternum 0.38 × as long as wide; suture absent. Abdomen 0.71 × as long as broad; sternite III with a circular, median, setigerous pore, which is 0.43 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.90 mm. Body 2.05 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.83 × as long as broad; anterior edge rounded. Elytra 1.27 × as long as broad and 1.62 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually blackish, less commonly reddish brown; elytra yellowish to black, usually reddish or reddish brown, with the base dark brown or black. The elytra are commonly lighter in color than the pronotum. Forms with bicolored elytra occur in the same populations with those having the elytra uniformly reddish brown or blackish. Pronotal tubercles in smaller males are barely developed, while in larger specimens they may be distinctly elevated and subacute at the apices. Size and dimensions vary as follows in a mixed lot of 14 ♂♂ and 14 ♀♀: TLmm: ♂ 1.42–1.97 (1.68 ± 0.050), ♀ 1.57–2.05 (1.79 ± 0.045); TL/EW ♂ 1.93–2.11 (2.02 ± 0.015), ♀ 1.91–2.12 (2.03 ± 0.015); PL/PW ♂ 0.79–0.91 (0.84 ± 0.009), ♀ 0.78–0.88 (0.85 ± 0.008); EL/EW ♂ 1.16–1.28 (1.21 ± 0.009), ♀ 1.20–1.29 (1.24 ± 0.009); EL/PL ♂ 1.39–1.61 (1.50 ± 0.022), ♀ 1.50–1.68 (1.58 ± 0.015). Total size range in material examined: 1.42 to 2.05 mm.

Distribution.—Southern United States, from south-central Texas to Florida, and the Greater Antilles from Cuba to Puerto Rico (see Fig. 30). About 80 specimens examined from the following localities: **UNITED STATES**: FLORIDA: Key West; PENNSYLVANIA: Philadelphia; TEXAS: Round Mt.; **WEST INDIES**: CUBA: Soledad (Cienfuegos), Cayamas, Havana; DOMINICAN REPUBLIC: St. Domingo, San Francisco Mts.; JAMAICA: Mandeville, Port Antonio; PUERTO RICO: Adjuntas. A series of 9 specimens collected in Philadelphia in 1898 may represent an isolated northern population, but the record is more likely to be an error. [AMNH, ANSP, CIN, MCZ, MNHN, USNM.]

Host fungi.—Fomes sclerodermeus [1], *Polyporus hydnoides* [1].

Discussion.—This is one of the largest and the most robust of the North American *Ceracis*. It is very similar to *C. nigropunctatus* in general form, antennal segmentation, and pronotal and elytral punctation, but it differs from that species in its larger size, shorter pronotum, and smooth and shiny surface. It is also quite similar to the West Indian *C. castaneipennis*, which is smaller and has 8-segmented antennae. The species has most often been confused with *C. multipunctatus* in collections, but the latter has much finer pronotal punctation and a rounded pronotal apex and smaller abdominal pore in the male.

The species was originally described by Mellié (1848) as *Ennearthron curtum* from "Havane" and *Cis obesus* from "Amerique boreale"; Dury (1917) redescribed it as *E. compacta* on the basis of material from Key West, Florida, and Round Mountain, Texas. The types of all three species are definitely conspecific.

Part of Dury's type species was bred from *Fomes marmoratus* (= *Fomes sclerodermeus*), and 3 specimens from Santo Domingo were apparently collected on *Pogonomyces hydnoides* (= *Polyporus hyd-*

noides). These are the only two host records known at present for this species.

C. curtus is obviously closely related to *C. nigropunctatus*, and the two species have been taken on the same species of fungi. Although the two occur together along the Gulf Coast of Texas, they are allopatric throughout most of their ranges. *C. curtus* is primarily a West Indian species and has been collected only a few times in North America; *C. nigropunctatus*, on the other hand, seems to be fairly common in Louisiana and Texas and extends through Mexico and Central America as far south as Panama. The scattered and rare occurrences of *C. curtus* in North America may indicate a relatively recent dispersal from the West Indies, possibly through the action of hurricanes. Further collecting in parts of Texas should determine whether or not it is established there and if it is reproductively isolated from *C. nigropunctatus*.

Ceracis dixiensis (Tanner), NEW COMBINATION

Octotemnus dixiensis Tanner, 1934: 47. Type locality: "Zion Nat'l. Park, Utah." Holotype, ♂, Tanner Coll., BYU.

Plesiotypes.— ♂ and ♀, ARIZONA: 15 mi. E Douglas, Cochise Co., Aug. 5, 1961, Lot 906 J. F. Lawrence, ex *Trametes hispida* on *Populus Fremontii* [MCZ].

Male.—Length 1.40 mm. Body 2.24 × as long as broad. Head and apex of pronotum reddish, remainder of pronotum dark reddish brown; elytra and ventral surfaces black; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex somewhat flattened; frontoclypeal ridge barely produced and emarginate, forming 2 weak, rounded tubercles. Antennae 8-segmented; segment III 2 × as long as IV. Pronotum 0.95 × as long as broad, widest just behind middle; sides weakly rounded; anterior edge weakly produced and emarginate; surface lightly granulate; punctures about 0.09 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.40 × as long as broad and 1.67 × as long as pronotum; sides subparallel for three-fourths of their lengths, gradually converging near apices; punctation dual and confused, coarser and denser than pronotal punctation, the punctures usually separated by less than 0.75 diameter, becoming confluent anteriorly, so that the surface appears rugose. Metasternum 0.50 × as long as wide; suture 0.20 × as long as median length of sternite. Abdomen 0.87 × as long as wide at base; sternite III with a transverse, median, setigerous pore, which is 0.69 × as long as wide, 0.55 × as long as body of sternite, indistinctly margined, and located just posterad of center.

Female.—Length 1.25 mm. Body 2.17 × as long as broad. Vertex as in male; frontoclypeal ridge simple. Pronotum 0.95 × as long as broad; anterior edge rounded. Elytra 1.39 × as long as broad and 1.78 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Pronotum yellowish orange to black, usually dark reddish brown or blackish, often with the apex reddish; elytra yellowish to black, usually black and occasionally reddish posteriorly near the suture. Anterior edge of pronotum varies slightly in the depth of the emargination, so that small males are almost indistinguishable from females on the basis of this character. Size and dimensions vary as follows in a series of 17 ♂ ♂ and 11 ♀ ♀ from 15 mi. E Douglas, Arizona (Lot 906): TLmm: ♂ 1.13–1.34 (1.23 ± 0.018), ♀ 1.13–1.30 (1.21 ± 0.013); TL/EW ♂ 2.17–2.35 (2.26 ± 0.014), ♀ 2.17–2.35 (2.30 ± 0.015); PL/PW ♂ 0.89–1.00 (0.95 ± 0.007), ♀ 0.89–1.00 (0.96 ± 0.009); EL/EW ♂ 1.36–1.50 (1.42 ± 0.011), ♀ 1.39–1.54 (1.47 ± 0.014); EL/PL ♂ 1.61–1.82 (1.70 ± 0.014), ♀ 1.63–2.00 (1.78 ± 0.030). Total size range in material examined: 1.01–1.39 mm.

Distribution.—Southwestern North America, from southern Utah to Guadalajara, Mexico, and from the Colorado River in California to the Big Bend Region in Texas (see Fig. 33). About 200 specimens have

been examined from the following localities: **UNITED STATES**: ARIZONA: 15 mi. E Douglas, 1 mi. N Nogales, 4 mi. NE Patagonia, 5 mi. SE Wickenburg; CALIFORNIA: 4 mi. E Blythe; NEW MEXICO: Dona Ana; TEXAS: Boquillas Camp (Big Bend National Park); UTAH: St. George, 3 mi. E Virgin, Zion National Park; **MEXICO**: JALISCO: Guadalajara. [BYU, CIN, CM, JFL, MCZ, USNM.]

Host fungi.—*Trametes hispida* [7(6)]; *Ganoderma* sp. [2].

Discussion.—This is a small, moderately elongate species with weakly developed pronotal and frontoclypeal characters in the male. In general appearance, it is similar to *C. powelli*, from which it differs by having 8-segmented antennae, finer pronotal punctation, and a larger abdominal pore. *C. obrieni* is the only other species with a large, transversely oval, abdominal pore in the male, but it differs from *C. dixiensis* in its much larger size and apically expanded elytra.

C. dixiensis occurs in the more arid portions of the Southwest, and it is normally found along river beds at low or middle elevations, in association with *Trametes hispida*, a common fungus on cottonwoods and willows. It is commonly associated with *Cis versicolor*, and in southern Arizona it has been collected with *Ceracis californicus* on both *T. hispida* and *Ganoderma* sp. The species has been collected in Jalisco and probably occurs throughout northern Mexico.

Ceracis minutissimus (Mellié), NEW COMBINATION
Fig. 18

Cis minutissimus Mellié, 1848: 334, pl. 11, fig. 12. Type locality: "Boston." Holotype, ♂, Pic Coll. (Chevrolat Coll.), MNHN.

Plesiotypes.— ♂ and ♀, MICHIGAN: Lapeer State Game Area, Lapeer Co., July 3, 1963, Lot 1197 J. F. Lawrence, ex *Daedalea unicolor* [MCZ].

Male.—Length 1.25 mm. Body 2.17 × as long as broad. Head and prothorax dark reddish brown, apex of pronotum brownish yellow; elytra, pectus, and abdomen blackish; legs, antennal funicle, and palpi yellowish, antennal club brownish. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge weakly produced and emarginate, forming 2 rounded tubercles. Antennae 8-segmented; segment III 1.5 × as long as IV. Pronotum 0.90 × as long as broad, widest at middle; sides strongly rounded; anterior edge produced and emarginate, forming 2 small, slightly elevated, approximate, triangular teeth; surface distinctly granulate; punctures about 0.05 × as large as scutellar base and separated by 1.5 to 2.5 diameters. Elytra 1.35 × as long as broad and 1.63 × as long as pronotum; sides weakly rounded, gradually diverging to about middle and converging posteriorly; punctation dual and confused, coarser and denser than pronotal punctation, the punctures usually separated by 0.75 diameter or less, becoming confluent anteriorly so that the surface appears rugose. Metasternum 0.50 × as long as wide; suture 0.17 × as long as median length of sternite. Abdomen 0.89 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.22 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.25 mm. Body 2.17 × as long as broad. Vertex somewhat flattened; frontoclypeal ridge simple. Pronotum 0.86 × as long as broad; anterior edge rounded. Elytra 1.39 × as long as broad and 1.78 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually dark reddish brown, almost always yellowish at apex; elytra yellowish to black, usually black, often somewhat reddish posteriorly along the suture. Anterior edge of pronotum barely produced in smaller males; distinctly produced in larger individuals, so that 2 distinct teeth are formed. Size and dimensions vary as

follows in a series of 22 ♂♂ and 23 ♀♀ from Lapeer Co., Michigan (Lot 1197): TLmm. ♂ 1.15–1.32 (1.22 ± 0.011), ♀ 1.00–1.32 (1.21 ± 0.016); TL/EW ♂ 2.00–2.29 (2.12 ± 0.013), ♀ 2.00–2.24 (2.11 ± 0.013); PL/PW ♂ 0.84–0.95 (0.88 ± 0.006), ♀ 0.81–0.90 (0.85 ± 0.006); EL/EW ♂ 1.26–1.48 (1.33 ± 0.011), ♀ 1.28–1.43 (1.36 ± 0.009); EL/PL ♂ 1.55–1.82 (1.68 ± 0.017), ♀ 1.68–1.94 (1.82 ± 0.013). Total size range in material examined: 0.97–1.42 mm.

Distribution.—Eastern United States from New Hampshire and Michigan to Alabama (see Fig. 32). More common in the northern part of the range, and to be expected in southern Canada. About 375 specimens have been examined from the following localities: ALABAMA: Mobile; INDIANA: La Porte Co., Smith Station; KENTUCKY: Mammoth Cave National Park; MASSACHUSETTS: Sherborn, Cambridge, Concord, Boston, Melrose, Stoneham; MICHIGAN: Lapeer State Game Area; NEW HAMPSHIRE: 7 mi. NW Wilton; NEW JERSEY: Morristown; OHIO: Cincinnati; PENNSYLVANIA: Chestnut Hill, Easton, Wissahickon Cr. [AMNH, CAS, CIN, CNC, CNHM, CU, HH, INHS, JFL, JS, MCZ, MNHN, UAL, UCD, USNM.]

Host fungi.—*Daedalea unicolor* [7(5)]; *Polyporus versicolor* [1]; *Polyporus adustus* [1].

Discussion.—This is one of the smaller species in the genus and is similar in size and general appearance to *C. minutus*, from which it may be distinguished by the coarser and denser elytral punctation, distinctly granulate and dull pronotal surface, and the presence of 2 approximate, triangular teeth on the pronotum of the male. It may be confused with smaller males and females of *C. thoracicornis*, but in the latter species the antennae are 9-segmented and the elytral punctation is finer and sparser.

Although specimens have been taken in Mobile, Alabama, the species appears to be more common in northeastern North America, where it normally feeds on the fungus *Daedalea unicolor*.

Ceracis minutus Dury
Fig. 19

Ceracis minuta Dury, 1917: 25. Type locality: "Palm Beach, Florida." Holotype, ♂, Dury Coll., CIN.

Plesiotypes.— ♂ and ♀, TEXAS: Brownsville, H. S. Barber, coll., ex *Ganoderma pseudoboletus* [USNM].

Male.—Length 1.12 mm. Body 2.14 × as long as broad. Head and apex of pronotum reddish; remainder of pronotum, elytra, and ventral surfaces dark reddish brown; legs, antennal funicle, and palpi yellowish, antennal club brownish. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 8-segmented; segment III 2.25 × as long as IV. Pronotum 0.95 × as long as broad, widest at middle; sides weakly rounded; anterior edge produced and deeply emarginate, forming 2 subparallel, slightly elevated horns, which are narrowly rounded at apices; disc slightly impressed just behind horns; surface lightly granulate; punctures about 0.12 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.24 × as long as broad and 1.37 × as long as pronotum; sides weakly rounded, diverging to about middle and gradually converging apically; punctation dual and subseriate, about as coarse and dense as pronotal punctation, the punctures usually separated by 1 diameter or more. Metasternum 0.44 × as long as wide; suture absent. Abdomen 0.76 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.20 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.02 mm. Body 2.16 × long as broad. Vertex somewhat flattened; frontoclypeal ridge simple. Pronotum 0.94 × as long as broad; anterior edge rounded.

Elytra 1.32 × as long as broad and 1.56 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to dark reddish brown, usually reddish or dark reddish brown, with the apex reddish; elytra yellowish to blackish, usually dark reddish brown, often with some reddish posteriorly near the suture. Anterior edge of pronotum in smaller males weakly produced and emarginate, forming 2 flattened, approximate teeth; in larger specimens, these are represented by longer, rounded horns, which are usually subparallel. Size and dimensions vary as follows in a series of 14 ♂♂ and 14 ♀♀ from Brownsville, Texas: TLmm: ♂ 0.92–1.12 (1.00 ± 0.013), ♀ 0.85–1.10 (0.97 ± 0.016); TL/EW ♂ 2.10–2.21 (2.14 ± 0.009), ♀ 2.05–2.17 (2.09 ± 0.011); PL/PW ♂ 0.87–0.94 (0.90 ± 0.007), ♀ 0.82–0.94 (0.88 ± 0.008); EL/EW ♂ 1.24–1.35 (1.28 ± 0.009), ♀ 1.25–1.39 (1.31 ± 0.010); EL/PL ♂ 1.41–1.64 (1.51 ± 0.017), ♀ 1.56–1.79 (1.66 ± 0.019). Total size range in material examined: 0.80–1.17 mm.

Distribution.—Southern Texas, Florida, and the Greater Antilles (see Fig. 33). About 175 specimens examined from the following localities: **UNITED STATES**: FLORIDA: Enterprise, Biscayne, Palm Beach, West Palm Beach, Key West; TEXAS: Brownsville; **WEST INDIES**: CUBA: Cayamas, Soledad (Cienfuegos); HAITI: Carrefour, Camp Perrin, Etang Sumatre, Port au Prince; JAMAICA: Port Antonio, Sav-la-Mar. [ANSP, BMNH, CIN, CM, MCZ, MNHN, USNM.]

Host fungi.—*Ganoderma* sp. [1].

Discussion.—This is the smallest species of *Ceracis* in the North American fauna and it differs from *C. minutissimus* in having 2 narrow pronotal horns in the male, finer and sparser elytral punctation, which tends to be subseriate, and a more lightly granulate and shiny pronotal surface. It is also very similar to the West Indian *C. variabilis* and the Mexican *C. militaris*. *C. variabilis* is a more narrow and elongate species with coarser and denser punctation. Further notes on this species group are given in a previous section.

Ceracis minutus is primarily a West Indian species, and it extends only into southern Florida and extreme southern Texas. The Texas series was apparently collected on "*Ganoderma pseudoboletus*" along with a series of *C. quadricornis* and *C. schaefferi*. The name *G. pseudoboletus* could not be traced in the mycological literature, but it probably represents one of the stipitate species of *Ganoderma*, such as *G. curtisii* or *G. lucidum*.

Ceracis monocerus, NEW NAME
Fig. 20

Enncarthron unicorne Casey, 1898: 90; Dury, 1917: 25. (Not *Ceracis unicornis* Gorham, 1898: 332). Type locality: "Florida." Holotype, ♂, Casey Coll., USNM.

Plesiotypes.— ♂ and ♀, FLORIDA: 4 mi. SE Lake Placid, Highlands Co., June 30, 1965, Lot 1532 J. F. Lawrence, ex *Polyporus sanguineus* [MCZ].

Male.—Length 1.25 mm. Body 2.17 × as long as broad. Head and prothorax reddish orange; elytra blackish anteriorly, yellowish posteriorly near the suture; pectus dark brown, abdomen yellowish brown; legs, antennal funicle, and palpi yellowish, antennal club brownish. Vertex with a broad, shallow, median impression; frontoclypeal ridge strongly produced, forming a long and narrow, slightly elevated, flattened, median horn, which is subtruncate at apex. Antennae 9-segmented; segment III 1.33 × as long as IV. Pronotum 0.82 × as long as broad, widest at middle; sides weakly rounded; anterior edge barely emarginate; surface distinctly granulate; punctures about 0.07 × as large as scutellar base and separated by 1.5 to 2.5 diameters. Elytra 1.39 × as long as broad and 1.78 × as long as pronotum; sides weakly rounded, diverging to about middle and gradually converging apically; punctation dual and confused, somewhat finer and about as dense as pronotal

punctation. Metasternum 0.50 × as long as wide; suture 0.44 × as long as median length of sternite. Abdomen 0.94 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.23 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.22 mm. Body 2.33 × as long as broad. Vertex somewhat flattened; frontoclypeal ridge simple. Pronotum 0.90 × as long as broad; anterior edge rounded. Elytra 1.48 × as long as broad and 1.72 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to dark reddish brown, usually reddish orange or reddish brown; elytra yellowish to black, usually blackish or brownish with varying amounts of yellowish or reddish posteriorly near the suture, the yellowish color occasionally occupying more than half of the dorsal surface. Frontoclypeal ridge in smaller males with a very short median projection; in larger specimens this is represented by a long, narrow horn, which is elevated and may extend well beyond the edge of the pronotum. The horn may be narrowly rounded, truncate, or expanded and shallowly emarginate at apex. Anterior edge of pronotum in males may be rounded to shallowly emarginate. Size and dimensions vary as follows in a series of 14 ♂ ♂ and 14 ♀ ♀ from Florida: TLmm: ♂ 1.00–1.30 (1.19 ± 0.021); ♀ 1.15–1.30 (1.23 ± 0.013); TL EW ♂ 2.10–2.26 (2.18 ± 0.013); ♀ 2.14–2.28 (2.21 ± 0.014); PL/PW ♂ 0.82–0.90 (0.86 ± 0.007); ♀ 0.84–0.90 (0.88 ± 0.007); EL EW ♂ 1.35–1.43 (1.38 ± 0.007), ♀ 1.36–1.48 (1.41 ± 0.004); EL PL ♂ 1.67–1.86 (1.73 ± 0.016), ♀ 1.72–1.87 (1.77 ± 0.012). Total size range in material examined: 1.00–1.30 mm.

Distribution.—Florida, Louisiana, and Cuba (see Fig. 30). About 65 specimens examined from the following localities: **UNITED STATES**: FLORIDA: 1 mi. SE Lake Placid; LOUISIANA: Killian; **WEST INDIES**: CUBA: no specific locality. [ANSP, IM, MCZ, USNM].

Host fungi.—*Polyporus sanguineus* [2 (1)].

Discussion.—As discussed in an earlier section, *C. monocerus* is a member of the *Ceracis furcifer* group, and it is easily distinguished from other North American species by the characters given in the key. It is most closely related to *C. cornifer* from Brazil, *C. hastifer* from Colombia, and *C. unicornis* from the Windward Islands, all of which have 9-segmented antennae and a frontoclypeal horn which is not bifurcate at the apex. *C. monocerus* is known only from Cuba and the extreme southern part of the eastern United States, but this distribution pattern suggests that it may be more widespread in the Greater Antilles. *C. unicornis* Gorham is a very similar form, and further collecting in the West Indies may well show that it is not distinct from *C. monocerus* even at the subspecific level. *C. cornifer* and *C. hastifer* are also very similar to *C. monocerus*, differing mainly in color and in the shape of the frontoclypeal horn and pronotal apex, and may not be specifically distinct.

Two small series of specimens from Florida and Louisiana were collected on the fungus *Polyporus sanguineus*. Both *C. furcifer* and *C. cornifer* have been collected on this same fungus.

The name *monocerus* is taken from the following two Greek words: *monos*, one, and *ceras*, horn.

Ceracis multipunctatus (Mellié), NEW COMBINATION

Fig. 24

Lmacanthron multipunctatum Mellié, 1848: 368, pl. 12, fig. 16; Jacquelin DuVal, 1857: 243. Type locality: "Cuba." Location of types unknown.

Plesiotypes.— ♂ and ♀, FLORIDA: Highlands Hammock State Park, Highlands Co., June 24, 1965, Lot 1504 J. F. Lawrence, ex *Ganoderma zonatum* [MCZ].

Male.—Length 1.47 mm. Body 2.11 × as long as broad. Head and pronotum black-

ish, apex of pronotum somewhat yellowish; elytra reddish, slightly darker on sides; ventral surfaces reddish brown; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex somewhat flattened; frontoclypeal ridge simple and rounded. Antennae 9-segmented; segment III 2 × as long as IV. Pronotum 0.88 × as long as broad, widest at posterior third; sides gradually converging anteriorly; surface distinctly granulate; punctures about 0.08 × as large as scutellar base and separated by 0.75 to 1.25 diameters. Elytra 1.29 × as long as broad and 1.57 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; Punctation single and relatively uniform, much coarser and denser than pronotal punctation, the punctures usually separated by 0.50 diameter or less. Metasternum 0.43 × as long as wide; suture barely indicated posteriorly. Abdomen 0.80 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.27 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.50 mm. Body 2.14 × as long as broad. Vertex and frontoclypeal ridge as in male. Pronotum 0.88 × as long as broad; anterior edge rounded. Elytra 1.32 × as long as broad and 1.61 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually black, with the apex often somewhat yellowish; elytra yellowish to blackish, usually reddish or dark reddish brown, usually unicolored and lighter in color than pronotum. Size and dimensions vary as follows in a series of 23 ♂ ♂ and 20 ♀ ♀ from Highlands Hammock State Park, Florida (Lot 1504): TLmm: ♂ 1.20–1.47 (1.33 ± 0.017), ♀ 1.20–1.50 (1.38 ± 0.018); TL/EW ♂ 2.00–2.12 (2.07 ± 0.009), ♀ 2.04–2.15 (2.09 ± 0.008); PL/PW ♂ 0.80–0.92 (0.85 ± 0.006), ♀ 0.80–0.88 (0.84 ± 0.006); EL/EW ♂ 1.23–1.35 (1.29 ± 0.006), ♀ 1.27–1.36 (1.32 ± 0.005); EL/PL ♂ 1.55–1.75 (1.64 ± 0.011), ♀ 1.59–1.82 (1.69 ± 0.014). Total size range in material examined: 1.17–1.75 mm.

Distribution.—Alabama, Florida, and the West Indies from Cuba to Montserrat (see Fig. 32). About 175 specimens examined from the following localities: **UNITED STATES**: ALABAMA: Mobile; FLORIDA: 4 mi. NE Copeland, Enterprise, Haulover, Highlands Hammock State Park, 2.5 mi. SE Lake City, 7 mi. SE Lake City, 4 mi. SE Lake Placid; **WEST INDIES**: CUBA: Buenos Aires (Trinidad Mts.), Cayamas, Guantanamo; JAMAICA: Ochos Rios, Mandeville; MONTSERRAT: The Cot. [AMNH, ANSP, CIN, CNHM, JFL, MCZ, USNM.]

Host fungi.—*Ganoderma zonatum* [7(4)]; *Fomes sclerodermeus* [1(1)]; *Polyporus supinus* [1].

Discussion.—This is a very short and broad species in which the pronotal and frontoclypeal modifications are completely lacking in the male. General form and punctation of the elytra are similar to *C. curtus*, *C. nigropunctatus*, and *C. castaneipennis*, but all three of these species have coarser and denser pronotal punctation and distinct tubercles on the pronotal apex in the male. *C. multipunctatus* resembles *C. obrieni* in having a strongly declined and finely and sparsely punctate pronotum, which is rounded in the male, but the latter species has 8-segmented antennae, dual elytral punctation, and a larger, transversely oval abdominal pore.

The identity of this species is still somewhat in doubt. The types should be in the Chevrolat Collection in Paris, but all of the specimens labeled as "multipunctatum" are from Santo Domingo rather than Cuba, and they are conspecific with *C. curtus*. A single specimen in the Marseul Collection is labeled "Ennearthron multipunctatum Mel. Cuba. . . . " and may be from the type series, but the specimen is a female and the pronotal punctation is somewhat coarser than that in the Florida specimens. In comparing the species with *curtus*, Mellié men-

tions that *multipunctatus* has finer punctation, especially on the prothorax. The pronotal punctation of the Marseul specimen is somewhat finer than in specimens of *curtus* but not as fine as that in the specimens here described as *multipunctatus*. Perhaps the examination of more West Indian specimens will clarify this situation.

This is another West Indian species which occurs only in Florida and Louisiana. In central Florida it was found breeding in *Fomes sclerodermeus* and *Ganoderma zonatum*, but it appears to be much more common in the latter.

Ceracis nigropunctatus NEW SPECIES
Fig. 16

Cis punctatus —, Gorham, 1883: 223. Misidentification.

Holotype.— ♂, LOUISIANA: 4 mi. S Grosse Tete, Iberville Parish, Dec. 4, 1965, Lot 1643 J. F. Lawrence, ex *Fomes sclerodermeus* [MCZ, No. 31284]. Allotype, ♀, same data [MCZ].

Male.—Length 1.47 mm. Body 2.18 × as long as broad. Head reddish, pronotum and major portion of elytra blackish, elytral suture reddish brown posteriorly; ventral surfaces reddish brown anteriorly, blackish posteriorly; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced and deeply emarginate, forming 2 subtriangular plates. Antennae 9-segmented; segment III 2.50 × as long as IV. Pronotum 0.89 × as long as broad, widest at middle; sides weakly rounded; anterior edge produced, forming 2 small, slightly elevated tubercles, which are separated by slightly more than a basal width; surface weakly granulate; punctures about 0.13 × as large as scutellar base and separated by 0.50 to 0.75 diameter. Elytra 1.30 × as long as broad and 1.46 × as long as pronotum; sides subparallel for most of their lengths, abruptly converging posteriorly; punctation single and relatively uniform, coarser and denser than pronotal punctation, the punctures usually separated by 0.33 diameter or less. Metasternum 0.40 × as long as wide; suture absent. Abdomen 0.83 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.50 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.45 mm. Body 2.19 × as long as broad. Vertex convex; frontoclypeal ridge simple. Pronotum 0.96 × as long as broad; anterior edge rounded. Elytra 1.31 × as long as broad and 1.48 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually dark brown or black; elytra yellowish to black, usually dark brown or black, never distinctly bicolored, but occasionally somewhat reddish posteriorly along the suture. Pronotal tubercles barely developed in smaller males; in larger individuals the tubercles are distinct and elevated and the pronotal disc is often somewhat bulging laterally. Size and dimensions vary as follows in a series of 28 ♂♂ and 21 ♀♀ from 4 mi. S Grosse Tete, Louisiana (Lot 1643): TLmm: ♂ 1.10–1.60 (1.37 ± 0.022), ♀ 1.20–1.55 (1.41 ± 0.018); TL/EW ♂ 2.00–2.26 (2.15 ± 0.011), ♀ 2.07–2.22 (2.14 ± 0.008); PL PW ♂ 0.82–0.96 (0.89 ± 0.006), ♀ 0.87–0.96 (0.93 ± 0.005); EL/EW ♂ 1.22–1.33 (1.28 ± 0.006), ♀ 1.22–1.33 (1.28 ± 0.006); EL/PL ♂ 1.37–1.67 (1.48 ± 0.012), ♀ 1.38–1.65 (1.49 ± 0.013). Total size range in material examined: 1.07–1.65 mm.

Paratypes.—100, LOUISIANA: same data as holotype [MCZ].

Distribution.—Louisiana and Texas south, through Mexico and Central America, to Panama (see Fig. 27). About 275 specimens examined from the following localities: **UNITED STATES**: LOUISIANA: 4 mi. S Grosse Tete; TEXAS: Columbus, Macdona, Palmetto State Park, San Antonio, Victoria, Wallisville; **MEXICO**: NAYARIT: San Blas; OAXACA: 8 mi. N. La

Ventosa; PUEBLA: 29 mi. E Xilotepec; TAMAULIPAS: Tampico; VERACRUZ: 11 mi. N Cordoba, Cotaxtla Expt. Sta., Cosamoloapan, 9 mi. NE Panuco, Veracruz; **CENTRAL AMERICA**: BRITISH HONDURAS: Manatee District; COSTA RICA: 4 mi. N Canas, Turrialba; EL SALVADOR: Los Choreos National Park; GUATEMALA: 6 mi. E Esquintla, Zapote; PANAMA: Barro Colorado. [BMNH, CAS, CNHM, JFL, MCZ, UCD, USNM.]

Host fungi.—*Polyporus hydnoides* [6(3)]; *Polyporus hirsutus* [2]; *Ganoderma* sp. [1]; *Fomes sclerodermeus* [1(1)].

Discussion.—This is a moderately short and broad species, which is similar to *C. curtus*, differing mainly in its smaller size, somewhat longer pronotum, and lightly granulate surface. It resembles darker specimens of *C. schaefferi* and *C. similis* (southern Baja California and western Mexico), but these two species have 8-segmented antennae, somewhat finer and sparser pronotal punctation, and a short, elevated, pronotal lamina in the male. *C. nigropunctatus* is fairly widely distributed in Mexico and Central America; it appears to exhibit no appreciable geographic variation, and the color of mature specimens is uniformly blackish or mahogany brown throughout the range. The species is sympatric with the closely related *C. curtus* in Texas, although the two have never been taken together.

The beetle has been found breeding in *Fomes sclerodermeus* and *Polyporus hydnoides*, but it appears to be more common in the latter. The 2 records from *P. hirsutus* are based on 1 or 2 specimens and may represent accidental occurrences.

The name *nigropunctatus* is taken from the Latin *niger*, black, and the Neolatin *punctatus*, punctate (originally punctum, a form of the verb *pungo*, to puncture).

Ceracis obrieni NEW SPECIES
Fig. 25

Holotype.—♂, ARIZONA: 2 mi. SW Patagonia, Santa Cruz Co., Sept. 3, 1961, Lot 953 J. F. Lawrence (C. W. O'Brien, coll.), ex *Polyporus gilvus* on *Populus Fremontii* [MCZ, No. 31285]. Allotype, ♀, same data [MCZ].

Male.—Length 1.60 mm. Body 2.06 × as long as broad. Head, pronotum, and posterior half of elytra reddish, anterior half of elytra blackish; ventral surfaces reddish brown; legs, antennal funicle, and palpi yellowish, antennal club brownish. Vertex slightly convex; frontoclypeal ridge simple and rounded. Antennae 8-segmented; segment III 2.33 × as long as IV. Pronotum 0.85 × as long as broad, widest at posterior fifth; sides gradually converging anteriorly; anterior edge strongly rounded; disc declined anteriorly; surface distinctly granulate; punctures about 0.08 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.35 × as long as broad and 1.91 × as long as pronotum; sides gradually diverging posteriorly for three-fourths of their lengths and abruptly converging near apices; punctation dual and somewhat confused, coarser and denser than pronotal punctation, the punctures usually separated by less than 0.75 diameter. Metasternum 0.56 × as long as wide; suture barely indicated posteriorly. Abdomen 0.94 × as long as wide at base; sternite III with a transverse, median, setigerous pore, which is 0.54 × as long as wide, 0.50 × as long as body of sternite, indistinctly margined, and located anterad of center.

Female.—Length 1.85 mm. Body 2.14 × as long as broad. Pronotum 0.84 × as long as broad. Elytra 1.40 × as long as broad and 1.88 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually reddish or reddish brown; elytra yellowish to black, almost always with some reddish posteriorly, and usually black with the posterior half reddish. Size and dimensions vary as follows in a series of 18 ♂♂ and 21 ♀♀ from 2 mi. SW Patagonia, Arizona: TLmm: ♂ 1.42–2.00 (1.70 ± 0.043), ♀ 1.45–1.87 (1.71 ±

0.024); TL EW ♂ 1.97–2.22 (2.09 ± 0.022), ♀ 2.00–2.23 (2.11 ± 0.014); PL/PW ♂ 0.77–0.95 (0.87 ± 0.014), ♀ 0.84–0.96 (0.91 ± 0.006); EL EW ♂ 1.28–1.42 (1.36 ± 0.012), ♀ 1.28–1.44 (1.35 ± 0.010); EL/PL ♂ 1.71–2.00 (1.86 ± 0.023), ♀ 1.68–2.00 (1.78 ± 0.016). Total size range in material examined 1.42–2.00 mm.

Paratypes.—ARIZONA: 23, same data as holotype [MCZ]; 14, same locality, Jan. 29, 1961, Lot 757 J. F. Lawrence (C. W. O'Brien, coll.), ex *Polyporus gilvus* on *Populus Fremontii* [MCZ].

Distribution.—Southeastern Arizona to southern Sinaloa (see Fig. 29). About 45 specimens examined from the following localities: **UNITED STATES**: ARIZONA: 2 mi. SW Patagonia; **MEXICO**: SINALOA: 8 mi. W El Palmito [MCZ].

Host fungi.—Polyporus gilvus [3(3)].

Discussion.—This is a large and very distinct species in which the elytra are expanded apically and both the pronotum and the frontoclypeal ridge are simple in the male. It is similar to *C. dixiensis* in having a large, transversely oval, abdominal pore, fine and sparse pronotal and coarse and dense elytral punctation, but that species is much smaller with subparallel elytra. *C. multipunctatus* has a similarly declined pronotal disc, which is finely and sparsely punctate and rounded apically in the male, but in that species the antennae are 9-segmented, the elytral punctation is single, and the abdominal pore is smaller and circular.

The species has been collected only in southern Arizona and southern Sinaloa, and in both localities it was breeding in *Polyporus gilvus*, an orange-brown fungus which may represent its headquarters. Although the range of the species traverses the more arid portions of northwestern Mexico, it is probable that *C. obrieni*, unlike *C. dixiensis*, prefers more mesic environments and is absent from most of the intervening area. Both of the localities from which it is recorded occur in regions of high summer rainfall, and the host fungus is most commonly encountered in the more humid parts of North America, such as the southeastern United States or the California coast, and in tropical Mexico.

The species is named in honor of Mr. Charles W. O'brien, whose collecting efforts have contributed greatly to my studies of the Ciidae.

Ceracis powelli NEW SPECIES
Fig. 23

Holotype.— ♂, ARIZONA: Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 3, 1961, Lot 892 J. F. Lawrence, ex *Polyporus abietinus* on conifer [MCZ, No. 31286]. Allotype, ♀, same data [MCZ].

Male.—Length 1.47 mm. Body 2.36 × as long as broad. Head and prothorax dark reddish brown; elytra, pectus, and abdomen blackish; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with a shallow, circular, median impression; frontoclypeal ridge weakly produced and emarginate, forming 2 rounded tubercles. Antennae 9-segmented; segment III 2 × as long as IV. Pronotum 0.86 × as long as broad, widest at posterior third; sides gradually converging anteriorly; anterior edge weakly produced and shallowly emarginate; surface distinctly granulate; punctures about 0.10 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.60 × as long as broad and 2.10 × as long as pronotum; sides subparallel anteriorly, gradually converging posteriorly; punctation dual and confused, coarser and denser than pronotal punctation, the punctures usually separated by less than 1 diameter, becoming confluent anteriorly, so that the surface appears rugose. Metasternum 0.62 × as long as wide; suture absent. Abdomen 0.93 ×as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.30 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.22 mm. Body 2.33 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.94 ×

as long as broad; anterior edge rounded. Elytra 1.57 × as long as broad and 2.06 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually either dark reddish brown to black or reddish; elytra yellowish to black, usually black with varying amounts of red posteriorly. All specimens from southern Arizona have a dark pronotum, whereas about two-thirds of the specimens from Durango have a reddish pronotum. Most individuals have a reddish fascia along the posterior part of the elytral suture, but in some specimens the entire apex is reddish. Pronotum in smaller males is indistinguishable from that of females, but in larger specimens the anterior edge is distinctly emarginate. Size and dimensions vary as follows in a series of 20 ♂♂ and 20 ♀♀ from 14 mi. SW El Salto, Durango, Mexico: TLmm: ♂ 1.22–1.55 (1.41± 0.021), ♀ 1.07–1.57 (1.36 ± 0.030); TL/EW ♂ 2.26–2.46 (2.35 ± 0.011), ♀ 2.21–2.45 (2.35 ± 0.013); PL/PW ♂ 0.85–0.95 (0.90 ± 0.007), ♀ 0.89–0.95 (0.92 ± 0.005); EL/EW ♂ 1.52–1.62 (1.57 ± 0.006), ♀ 1.46–1.64 (1.57 ± 0.009); EL/PL ♂ 1.94–2.10 (2.02 ± 0.010), ♀ 1.94–2.11 (2.01 ± 0.010). Total size range in material examined: 1.07–1.57 mm.

Paratypes.—ARIZONA: 6, Rustler Park, 8 mi. W Portal, Cochise Co., Aug. 3, 1961, Lot 892 J. F. Lawrence, ex *Polyporus abietinus* on conifer [MCZ]; DURANGO: 9, 9 mi. E La Ciudad, July 23, 1964, Lot 1311 J. F. Lawrence (J. Powell, coll.), ex *Polyporus pargamenus* on *Quercus* sp. [MCZ]; 200, 14 mi. SW El Salto, June 20, 1964, E. E. Lindquist, coll., ex "*Polyporus*" on pine [CNC].

Distribution.—Southeastern Arizona and southern Durango (see Fig. 27). About 225 specimens examined from the following localities: **UNITED STATES**: ARIZONA: Miller Canyon (10 mi. W Hereford), Rustler Park (8 mi. W Portal); **MEXICO**: DURANGO: 9 mi. E La Ciudad, 14 mi. SW El Salto. [CNC, JFL, MCZ.]

Host fungi.—*Polyporus abietinus* [2(1)]; *Polyporus pargamenus* [1].

Discussion.—This is an elongate and narrow species with weakly developed pronotal and frontoclypeal characters in the male. It is superficially similar to *C. dixiensis*, from which it differs by having 9-segmented antennae, somewhat coarser pronotal punctation, and a smaller, circular abdominal pore. It also resembles smaller specimens of *C. californicus*, from which it may be distinguished by the somewhat finer and more confused elytral punctation, shorter 3rd antennal segment, and the shorter pronotum, which is narrowed anteriorly.

C. powelli is known only from intermediate and high elevations in the mountains of southern Arizona and northern Mexico (Huachuca Mts., Chiricahua Mts., and Sierra Madre Occidental), where it has been collected in association with *Polyporus abietinus* on pine and the related *P. pargamenus* on oak. In southern Arizona, the species is sympatric with both *C. dixiensis* and *C. californicus*, and the three may occur together in the canyons at middle elevations. The preference of *C. californicus* for species of *Ganoderma* and of *C. dixiensis* for *Trametes hispida* probably reduces competition among the three species.

This species is named for Dr. Jerry A. Powell who has collected a number of interesting Ciidae in western North America and Mexico.

Ceracis pullulus (Casey) NEW COMBINATION
Fig. 22

Ennearthron pullulum Casey, 1898: 90; Dury, 1917: 25; Blatchley, 1918: 54. Type locality: "Florida." Holotype, ♂, Casey Coll., USNM.

Plesiotypes.—♂ and ♀, FLORIDA: Highlands Hammock State Park, Highlands Co., June 24, 1965, Lot 1501 J. F. Lawrence, ex *Polyporus licnoides* [MCZ].

Male.— Length 1.47 mm. Body 2.56 × as long as broad. Head and prothorax dark

reddish brown; elytra blackish with a narrow reddish band along suture; ventral surfaces blackish; legs, antennal funicle, and palpi brownish yellow, antennal club dark brown. Vertex with a deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 9-segmented; segment III 2 × as long as IV. Pronotum 1.09 × as long as broad, widest at middle; sides subparallel; anterior edge produced, forming a flat, slightly elevated lamina, which is deeply emarginate, giving the appearance of 2 slightly divergent, rounded horns; disc impressed anteriorly just behind lamina and bearing a short, transverse carina on each side of it; surface distinctly granulate; punctures about 0.09 × as large as scutellar base and separated by 1.0 to 2.0 diameters. Elytra 1.48 × as long as broad and 1.36 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; punctation dual and distinctly seriate, the larger punctures forming relatively straight rows. Metasternum 0.52 × as long as wide; suture absent. Abdomen 0.85 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.33 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.42 mm. Body 2.48 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 1.00 × as long as broad; anterior edge rounded. Elytra 1.56 × as long as broad and 1.71 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually dark reddish brown, often with the apex reddish; elytra yellowish to black, usually black with some reddish mesially along the suture. In smaller males, the pronotum is more rounded laterally and the anterior edge is weakly produced and emarginate, forming [illegible] subtriangular plates. In larger individuals the sides of the pronotum are subparallel and the apex is strongly and abruptly produced and deeply emarginate; the resulting horns are always broad and rounded at apices and may be subparallel or diverging. Surface of pronotum may be lightly or more distinctly granulate. Size and dimensions vary as follows in a series of 28 ♂ ♂ and 20 ♀ ♀ from Highlands Hammock State Park, Florida (Lot 1501): TLmm: ♂ 1.12–1.57 (1.38 ± 0.021), ♀ 1.07–1.52 (1.34 ± 0.025); TL/EW ♂ 2.23–2.58 (2.44 ± 0.014), ♀ 2.15–2.48 (2.28 ± 0.016); PL/PW ♂ 0.95–1.11 (1.05 ± 0.008), ♀ 0.87–1.00 (0.93 ± 0.006); EL/EW ♂ 1.36–1.50 (1.43 ± 0.008), ♀ 1.35–1.56 (1.44 ± 0.011); EL/PL ♂ 1.30–1.58 (1.42 ± 0.014), ♀ 1.64–1.85 (1.73 ± 0.012). Total size range in material examined: 1.03–1.62 mm.

Distribution.—Southern Coastal Plain and Gulf Coast of North America, from North Carolina south to Florida and west to Louisiana: Greater Antilles from Cuba to Puerto Rico (see Fig. 28). About 400 specimens examined from the following localities: **UNITED STATES**: ALABAMA: Mobile; FLORIDA: Chipola Park (Dead Lake), Enterprise, Haulover, Highlands Hammock State Park (6 mi. W Sebring), Key West, 2.5 mi. SE Lake City, 7 mi. SE Lake City, 4 mi. SE Lake Placid, 18 mi. SE Paradise Key, Pennekamp State Park (Key Largo); GEORGIA: Savannah; LOUISIANA: Audubon State Park, 4 mi. S Grosse Tete, 5 mi. S Livingston; NORTH CAROLINA: Magnolia, Randolph Co.; SOUTH CAROLINA: Moncks Corners, Yemassee; **WEST INDIES**: CUBA: Buenos Aires (Trinidad Mts.), Mina Carlotta (Trinidad Mts.), Soledad (Cienfuegos); JAMAICA: Kingston; PUERTO RICO: Cidra. [ANSP, BMNH, CAS, CIN, CNHM, JFC, MCZ, USNM.]

Host fungi.—*Polyporus gilvus* [7(3)]; *Polyporus lienoides* [4(4)]; *Ganoderma zonatum* [4(2)]; *Ganoderma* sp. [2(2)]; *Polyporus iodinus* [2(1)]; *Polyporus hydnoides* [1]; *Fomes igniarius* [1].

Discussion.—This species is similar in

size, form, and antennal segmentation to *C. thoracicornis* and *C. cucullatus*, but it is easily distinguished from both by the seriate elytral punctation. *C. singularis* also has the elytral punctures arranged in distinct rows, but it differs from *C. pullulus* in having 10-segmented antennae and distinctive pronotal horns in the male.

Assuming that the Philadelphia record for *C. curtus* is erroneous, *Ceracis pullulus* is the only West Indian species to extend along the Southern Coastal Plain as far as North Carolina. It is fairly common in central Florida, where it normally occurs on *Polyporus gilvus* and its relatives. In these fungi it may be associated with *Ceracis singularis*, *C. punctulatus*, and *Brachycis brevicollis* Casey.

In a series of about 100 specimens collected on *Ganoderma* sp. in Pennekamp State Park, Key Largo, Florida, no males could be found. It is possible that this represents a parthenogenetic population. Parthenogenesis is known in at least one other species of Ciidae, *Cis fuscipes* Mellié (Lawrence, 1967).

Ceracis punctulatus punctulatus Casey

Ceracis punctulata Casey, 1898: 90; Dury, 1917: 26; Blatchley, 1918: 54. Type locality: "Florida." Holotype, ♂, Casey Coll., USNM.

Plesiotypes.— ♂ and ♀, FLORIDA: 16 mi. W Miami, Dade Co., June 28, 1965, Lot 1528 J. F. Lawrence, ex *Polyporus hydnoides* on *Casuarina* sp. [MCZ].

Male.—Length 1.42 mm. Body 2.28 × as long as broad. Head and prothorax reddish brown; elytra, pectus, and abdomen brownish black; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 8-segmented; segment III 2 × as long as IV. Pronotum 0.96 × as long as broad, widest at middle; sides weakly rounded; anterior edge produced, forming a flat, slightly elevated lamina, which is deeply emarginate, giving the appearance of 2 slightly diverging, subtriangular horns; disc impressed anteriorly just behind lamina and bearing a short, transverse carina on each side of it; surface lightly granulate; punctures about 0.11 × as large as scutellar base and separated by 0.5 to 1.0 diameter. Elytra 1.36 × as long as broad and 1.48 × as long as pronotum; sides subparallel for most of their lengths and abruptly converging near apices; punctation dual and confused, somewhat finer and sparser than pronotal punctation, the punctures often separated by 1 diameter posteriorly, becoming denser anteriorly. Metasternum 0.55 × as long as wide; suture barely indicated posteriorly. Abdomen 0.90 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.40 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.37 mm. Body 2.29 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.95 × as long as broad, widest behind middle; anterior edge rounded. Elytra 1.42 × as long as broad and 1.62 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually reddish brown or dark brown; elytra yellowish to black, usually dark brown or black, almost always unicolored, but occasionally reddish posteriorly near the suture and resembling *C. punctulatus rubriculus*. The most commonly observed form is that with the pronotum dark reddish brown and the elytra black. Anterior edge of pronotum in smaller males barely produced and emarginate, so that 2 tubercles are formed; in larger males the pronotum bears 2 distinct, subtriangular horns, which may be diverging. Size and dimensions vary as follows in a series of 25 ♂ ♂ and 25 ♀ ♀ from 16 mi. W Miami, Florida (Lot 1528): TLmm: ♂ 1.20–1.55 (1.38 ± 0.022), ♀ 1.05–1.52 (1.33 ± 0.022); TL/EW ♂ 2.13–2.38 (2.27 ± 0.014), ♀

2.07–2.30 (2.19 ± 0.013); PL PW ♂ 0.90–1.04 (0.95 ± 0.006), ♀ 0.86–0.96 (0.92 ± 0.006); EL EW ♂ 1.27–1.41 (1.35 ± 0.008), ♀ 1.30–1.45 (1.36 ± 0.009); EL/PL ♂ 1.37–1.63 (1.48 ± 0.015), ♀ 1.55–1.76 (1.66 ± 0.013). Total size range in material examined: 1.05–1.65 mm.

Distribution.—Apparently restricted to Florida and intergrading with *rubriculus* in northern Florida and Georgia (see Fig. 34). About 200 specimens examined from the following localities: FLORIDA: Archbold Biological Station, Biscayne, Dunedin, Enterprise, Highlands Hammock State Park (6 mi. W Sebring), 13 mi. N Homestead, 7 mi. SE Lake City, 4 mi. SE Lake Placid, Miami, 16 mi. W Miami, Tampa. Probable intergrades seen from Chipola Park (Dead Lake), Calhoun Co., Florida, and Savannah, Georgia. [CIN, CNHM, CU, JFL, MCZ, UAL, USNM.]

Host fungi.—*Polyporus hydnoides* [5(4)]; *Polyporus licnoides* [2(2)]; *Ganoderma zonatum* [2(1)]; *Polyporus gilvus* [2]; *Ganoderma* sp. [1].

Discussion.—This species is very similar to *Ceracis sallei*, from which it may be distinguished by the somewhat coarser and denser pronotal punctation and the circular abdominal pore in the male. *C. schaefferi* is also similar in general appearance but differs by having much coarser and denser elytral punctation and finer and sparser pronotal punctation. The typical southern form is rare in collections and has often been confused with other species. A series of specimens from Massachusetts were determined as *C. punctulatus* and distributed to various museums by C. A. Frost; these specimens are all *C. minutissimus*.

Ceracis punctulatus is distributed throughout eastern North America, but the typical subspecies occurs only in central and southern Florida. It has been found breeding in *Polyporus hydnoides* and *Ganoderma zonatum* where it was associated with *Ceracis sallei* and *C. multipunctatus*, and in *Polyporus licnoides* along with *C. pallidus*. It is interesting that the southern race occurs with the related *C. sallei* in two different fungi, whereas the northern race, *rubriculus*, has never been collected with that species, although the two are sympatric over most of eastern North America.

A single dark specimen was collected at Chipola Park, Florida, along with 9 typical bicolored *rubriculus* on *P. gilvus*, and a few specimens in a series from Savannah, Georgia, have the red color on the elytra very much reduced. These probably represent intergrades. It is probable that *C. punctulatus punctulatus* represents a population isolated in central Florida during the Pleistocene inundation of the Southern Coastal Plain. Howden (1963) discusses the effects of these Pleistocene events on flightless Scarabaeidae. The black phenotype apparently originated in and spread through the island population, which, upon the reconnection of Florida with the mainland, spread northward and came into contact with the bicolored northern form. Further collecting in Georgia and northern Florida will be necessary to determine the extent to which the two forms are reproductively compatible.

Ceracis punctulatus rubriculus NEW SUBSPECIES

Fig. 13

Ceracis sallei Mellié (in part), Weiss, 1919: 144; Weiss and West, 1920: 8; Weiss and West, 1921: 169.

Ceracis sp., Gahan, 1927: 30; Graves, 1960: 66 (in part).

Holotype.— ♂, MISSOURI: 10 mi. S Columbia, Boone Co., Aug. 26, 1964, Lot 1348 J. F. Lawrence, ex *Polyporus gilvus* [MCZ, No. 31283]. Allotype, ♀, same data [MCZ].

Male.—Length 1.52 mm. Body 2.26 × as long as broad. Head and apex of pronotum reddish, remainder of pronotum dark reddish brown; elytra black anteriorly, posterior three-fifths reddish orange; prosternum and abdomen dark reddish brown, pectus black; legs, antennal funicle, and palpi brownish yellow, antennal club dark brown.

Vertex with a deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antenna 8-segmented; segment III 2 × as long as IV. Pronotum 0.93 × as long as broad, widest at middle; sides weakly rounded; anterior edge produced, forming a flat, slightly elevated lamina, which is deeply emarginate, giving the appearance of 2 subtriangular horns; disc impressed anteriorly just behind lamina and bearing a short, transverse carina on each side of it; surface lightly granulate; punctures about 0.12 × as large as scutellar base and separated by 0.5 to 1.0 diameter. Elytra 1.33 × as long as broad and 1.44 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; punctation dual and confused, somewhat finer and sparser than pronotal punctation, the punctures often separated by 1 diameter posteriorly, becoming denser anteriorly. Metasternum 0.50 × as long as wide; suture barely indicated posteriorly. Abdomen 0.87 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.41 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.50 mm. Body 2.14 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.88 × as long as broad, widest behind middle; anterior edge rounded. Elytra 1.36 × as long as broad and 1.73 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usualy dark reddish brown or black, often with the apex reddish; elytra yellowish to black, almost always black with a reddish orange, posteromesal patch, which varies in size but usually occupies less than two-thirds of the dorsal surface, occasionally reduced as in *C. punctulatus punctulatus*. Anterior edge of pronotum in smaller males barely produced and emarginate, so that 2 tubercles are formed; in larger males the pronotum bears 2 distinct, subtriangular horns, which may be subparallel or diverging. Size and dimensions vary as follows in a series of 36 ♂ ♂ and 35 ♀ ♀ from 10 mi. S Columbia, Missouri (Lot 1348): TLmm: ♂ 1.27–1.70 (1.44 ± 0.017), ♀ 1.25–1.55 (1.42 ± 0.012); TL/EW ♂ 2.11–2.31 (2.21 ± 0.010), ♀ 2.07–2.27 (2.17 ± 0.007); PL/PW ♂ 0.88–1.00 (0.94 ± 0.005), ♀ 0.84–0.96 (0.90 ± 0.005); EL/EW ♂ 1.23–1.39 (1.32 ± 0.006), ♀ 1.30–1.42 (1.37 ± 0.005); EL/PL ♂ 1.35–1.68 (1.49 ± 0.012), ♀ 1.56–1.89 (1.72 ± 0.012). Total size range in material examined: 1.20–1.75 mm.

Paratypes.—70, MISSOURI: same data as holotype [MCZ].

Distribution.—Eastern United States, from Michigan and southern Vermont to southern Texas and northern Florida, east of the 100th meridian; a single specimen recorded from western Cuba (see Fig. 34). About 800 specimens examined from the following localities: **UNITED STATES**: ALABAMA: Mobile, 10 mi. S Mobile, Selma; ARKANSAS: Hope, Washington Co.; DISTRICT OF COLUMBIA: Washington, Takoma Park; FLORIDA: Chipola Park (Dead Lake); GEORGIA: Savannah, Waycross; ILLINOIS: Carterville, Glen View, Plano, Springfield, Urbana, Willow Springs; INDIANA: Beverley Shores, Dune Areas (Porter Co.), Thayer; IOWA: Cedar Rapids; KANSAS: 5 mi. S Lawrence; KENTUCKY: near Cincinnati, Mammoth Cave National Park; LOUISIANA: Audubon State Park, 4 mi. S Grosse Tete, Harahan, 5 mi. S Livingston; MARYLAND: Beltsville, Bladensburg, Branchville, College Park, Great Falls, Jackson's Island, Plummer's Island, Sparrows Point; MASSACHUSETTS: Naushon Island; MICHIGAN: Ann Arbor, Lapeer State Game Area, Richfield Center; MISSISSIPPI: 15 mi. N Ackerman, Lucedale, 4 mi. W Starkville; MISSOURI: 3 mi. SW Arbor, 10 mi. S Columbia, St. Louis; NEW JERSEY: Anglesea, Arlington, Chester, Clementon, Middlebush, Midvale, Montclair, Springfield; NEW YORK: Fort Niagara, Ithaca, Mo-

sholu, New Rochelle, New York, Staten Island, West Point, Orient; NORTH CAROLINA: Beaufort, 1 mi. SW Brevard, Joyce Kilmer Forest, Magnolia, Raleigh, ¾ mi. SE Rocky Knob, Southern Pines, Tryon; OHIO: Cincinnati; PENNSYLVANIA: Chestnut Hill, Easton, Harrisburg, Mt. Moriah, Twin Lakes, Upper Darby, Wissahickon Cr.; SOUTH CAROLINA: Pawley's Beach; TENNESSEE: Bledsoe State Forest, Gatlinburg; TEXAS: Brownsville, Huntsville, Kerrville, San Antonio, Wallisville; VIRGINIA: Arlington, Clapham Junction, Falls Church, Occoquan; VERMONT: East Dorset; **WEST INDIES**: CUBA: Banos de San Vicente. [AMNH, ANSP, BMNH, CAS, CIN, CNC, CNHM, INHS, JFC, JFL, KU, MCZ, UAL, UCD, USNM.]

Host fungi.—Polyporus gilvus [32(13)]; *Polyporus hydnoides* [2]; *Ganoderma lucidum* [1]; *Ganoderma* sp. [1]; *Polyporus radiatus* [1]; *Fomes fomentarius* [1]; *Polyporus adustus* [1]; *Polyporus hirsutus* [1]; *Polyporus pargamenus* [1].

Discussion.—This subspecies differs from *C. punctulatus punctulatus* mainly in the color of the elytra, which are reddish orange posteriorly. *C. punctulatus rubriculus* has often been confused with *C. sallei* in collections and in the literature, because of the similarity of coloration between the two. *C. sallei* also has bicolored elytra, but the reddish color is usually more extensive, occupying two-thirds of the surface, and the pronotum is often more reddish. In addition, *C. sallei* has finer and sparser pronotal punctation and a transverse abdominal pore. A number of Weiss' records of *C. sallei* are based on specimens of *rubriculus*.

C. punctulatus rubriculus ranges over most of eastern North America and intergrades with *C. punctulatus punctulatus* in Georgia and northern Florida. It is more common in the southern part of the range and has not been collected in Canada or northern New England. The single specimen apparently found on *P. pargamenus* in Vermont may be a contaminant from a collection from Naushon Island, Massachusetts —the two were stored together for a time in Vermont. A specimen of *rubriculus* from western Cuba may represent a recent dispersal from southern Louisiana.

There is good evidence for a strong preference for *Polyporus gilvus*, since every other record above consists of a single adult specimen. This beetle is the most common and characteristic inhabitant of *P. gilvus* in eastern North America, and it may be found in association with *Ceracis singularis*, *C. pullulus*, *Brachycis brevicollis* Casey, and the tenebrionid beetle *Platydema ellipticum*. Throughout the same area, the closely related *C. sallei* occurs almost exclusively on *Ganoderma applanatum*. In Florida, however, there is less evidence of host preference in either species, and *C. sallei* has been collected on several occasions in the same fruiting body with *C. punctulatus punctulatus*. I think this suggests that host specificity played an important role in the evolution of *sallei* and *punctulatus* (the original monotypic species) from a common ancestor and that the situation in Florida represents a secondary breakdown of this mechanism. If the two ancestral populations had become geographically isolated long enough to produce a divergence in their genetic systems and then had reestablished contact, the evolution of a different food preference in each would greatly reduce the incidence of cross breeding and the accompanying disadvantages of hybrid inviability or hybrid sterility. When these patterns of host selection behavior had become fixed, the two species were free to spread throughout eastern North America and become completely sympatric but ecologically isolated. Both species spread into Florida, and then in the Pleistocene the Florida populations were isolated from the mainland. This isolation from the main gene pool, which was accompanied by a relatively rapid morphological change (decrease in size in *sallei*), may have also led to changes in food preference. If the two species were now reproductively in-

compatible, perhaps through differences in sexual behavior, then there would be no selective pressure against the development of similar food preferences. The genetics of island or founder populations is discussed at length in Mayr (1963).

The name *rubriculus* is derived from the Latin *ruber*, red, and the Latin *culus*, rump.

Ceracis quadricornis Gorham
Fig. 17

Ceracis quadricornis Gorham, 1886: 359. Type locality: "Mexico, Tuxtla." Holotype, ♂, BMNH.

Plesiotypes.— ♂ and ♀, TEXAS: Brownsville, H. S. Barber, coll., ex *Ganoderma pseudoboletus* [USNM].

Male.—Length 1.27 mm. Body 2.55 × as long as broad. Head and apex of pronotum reddish brown, remainder of pronotum blackish brown; elytra and ventral surfaces dark reddish brown; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 8-segmented; segment III 2 × as long as IV. Pronotum 1.10 × as long as broad, widest at anterior third; sides gradually converging posteriorly; anterior edge produced and deeply emarginate, forming 2 divergent, slightly elevated horns, which are weakly carinate above and narrowly rounded at apices; disc slightly impressed just behind and between the horns and bearing a short, transverse carina laterad of each; surface distinctly granulate; punctures about 0.07 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.53 × as long as broad and 1.32 × as long as pronotum; sides subparallel for most of their lengths, abruptly converging near apices; punctation dual and confused, coarser and denser than pronotal punctation, the punctures usually separated by less than 1 diameter. Metasternum 0.53 × as long as wide; suture barely indicated posteriorly. Abdomen 0.81 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.23 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.20 mm. Body 2.40 × as long as broad. Vertex somewhat flattened; frontoclypeal ridge simple. Pronotum 1.00 × as long as broad, widest behind middle; anterior edge rounded. Elytra 1.50 × as long as broad and 1.67 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually dark reddish brown or blackish, with the apex reddish; elytra yellowish to black, usually dark reddish brown or black. Sides of pronotum in females and smaller males subparallel or slightly converging anteriorly; in larger males the sides diverging to apical third. Anterior edge of pronotum in smaller males bearing 2 approximate teeth; in larger males these are represented by 2 distinct horns, which may be flat or carinate and straight or slightly diverging. Size and dimensions vary as follows in a series of 14 ♂♂ and 14 ♀♀ from Brownsville, Texas: TLmm: ♂ 1.05–1.32 (1.17 ± 0.022), ♀ 0.97–1.20 (1.09 ± 0.019); TL/EW ♂ 2.44–2.67 (2.57 ± 0.021), ♀ 2.35–2.55 (2.43 ± 0.014); PL/PW ♂ 1.05–1.15 (1.09 ± 0.008), ♀ 0.93–1.00 (0.97 ± 0.008); EL/EW ♂ 1.44–1.55 (1.50 ± 0.008), ♀ 1.50–1.61 (1.55 ± 0.010); EL/PL ♂ 1.30–1.47 (1.40 ± 0.015), ♀ 1.67–1.86 (1.74 ± 0.014). Total size range in material examined: 0.96–1.35 mm.

Distribution.—Southern Texas, through eastern and southern Mexico and as far south as Costa Rica (see Fig. 30). About 275 specimens examined from the following localities: **UNITED STATES**: TEXAS: Brownsville; **MEXICO**: CHIAPAS: 24 mi. NW Huixtla, 9 mi. N Arriaga; OAXACA: 48 mi. E La Ventosa; PUEBLA: 29 mi. E Xilotepec; TAMAULIPAS: Tampico; VER-

ACRUZ: El Fortin, Tuxpango, San Juan de la Punta, Tierra Blanca, 9 mi. NE Panuco, Tejeria, Cordova, Veracruz, Tuxtla, Cotaxtla Experiment Station; **CENTRAL AMERICA**: COSTA RICA: 4 mi. N Canas, Turrialba; GUATEMALA: 4 mi. E Cuilapa, 6 mi. E Esquintla; NICARAGUA: 20 mi. SE Leon, 5 mi. N Esteli. [BMNH, CAS, CNHM, JFL, MCZ, USNM.]

Host fungi.—*Polyporus occidentalis* [5 (3)]; *Polyporus hirsutus* [2(1)]; *Polyporus maximus* [2(1)]; *Polyporus hydnoides* [2(1)]; *Trametes corrugata* [1(1)]; *Lenzites striata* [1(1)]; *Ganoderma* sp [1].

Discussion.—This is a very small, narrow, and elongate species with 2 narrow, diverging pronotal horns in the male. The general form and secondary sexual characters are similar to *C. thoracicornis* and *C. bicornis*, both of which have 9-segmented antennae. The elytral punctation is similar to that in *C. minutus*, but that species is shorter and broader in form. *C. dixiensis* and *C. minutissimus* differ by having coarser and denser elytral punctation and different pronotal modifications in the male.

Ceracis quadricornis is a tropical Mexican species which extends into the United States only as far as southern Texas. Although the Texas series was taken on an unknown *Ganoderma* ("pseudoboletus"), Mexican records indicate that the species prefers fungi in the *Polyporus versicolor* group, such as *P. occidentalis*, *P. hirsutus*, and *P. maximus*.

Ceracis sallei Mellié
Fig. 11

Lunacanthion Ceracis sallei Mellié, 1848: 377, pl. 12, fig. 22; Casey, 1898: 90; Blatchley, 1910: 900; Duvy, 1917: 26. Type locality: "Nouvelle Orleans." Lectotype ♂, Oberthür Coll. (Salle Coll.) MNHN.

Ceracis sallei: Gorham, 1894: 66.

Plesiotypes.— ♂ and ♀, MASSACHUSETTS: Belmont, Middlesex Co., July 3, 1966, Lot 1816 J. F. Lawrence, ex *Ganoderma applanatum* [MCZ].

Male.—Length 1.72 mm. Body 2.38 × as long as broad. Head, maxillary palpi, and pronotum reddish brown; anterior third of elytra blackish brown, posterior two-thirds reddish yellow; ventral surfaces blackish; legs and antennal funicle brownish yellow, antennal club brownish. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 8-segmented; segment III 2 × as long as IV. Pronotum 1.00 × as long as broad, widest at middle; sides subparallel; anterior edge produced, forming a flat, slightly elevated lamina, which is deeply emarginate, giving the appearance of 2 slightly divergent, subtriangular horns; disc impressed anteriorly just behind lamina and bearing a short, transverse carina in each side of it; surface distinctly granulate; punctures about 0.10 × as large as scutellar base and separated by 0.75 to 1.25 diameters. Elytra 1.38 × as long as broad and 1.38 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; punctation dual and confused, about as coarse and dense as pronotal punctation, the punctures somewhat denser anteriorly. Metasternum 0.64 × as long as wide; suture about 0.18 × as long as median length of sternite. Abdomen 0.84 × as long as wide at base; sternite III with a transverse, median, setigerous pore, which is 0.83 × as long as wide, 0.45 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.52 mm. Body 2.18 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.96 × as long as broad; anterior edge rounded. Elytra 1.32 × as long as broad and 1.54 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to blackish, usually either reddish or dark reddish brown; elytra yellowish to black, with the posterior portion reddish or reddish yellow. The pronotum is almost

always lighter in color than the posterior part. The reddish pigment on the elytra varies considerably, but it usually occupies more than half of the surface and often extends almost to the base mesially. Smaller males have the sides of the pronotum more rounded and the anterior edge barely emarginate, while larger specimens tend to have a parallel-sided pronotum with a distinct lamina anteriorly. The lamina varies in its width and in the depth and shape of the emargination, so that 2 small triangular teeth, 2 broad rounded horns, or 2 narrower diverging horns may be formed. In smaller individuals, the lamina may be less abrupt laterally and the transverse carinae may be absent. Size and dimensions vary as follows in a series of 25 ♂♂ and 25 ♀♀ from Belmont, Massachusetts (Lot 1816): TLmm: ♀ 1.25–1.72 (1.47 ± 0.029), ♀ 1.12–1.67 (1.42 ± 0.026); TL/EW ♂ 2.08–2.39 (2.27 ± 0.017), ♀ 2.09–2.29 (2.20 ± 0.010); PL/PW ♂ 0.87–1.00 (0.97 ± 0.007), ♀ 0.88–0.96 (0.93 ± 0.005); EL/EW ♂ 1.25–1.43 (1.35 ± 0.008), ♀ 1.28–1.43 (1.36 ± 0.008); EL/PL ♂ 1.37–1.65 (1.47 ± 0.016), ♀ 1.50–1.74 (1.62 ± 0.013). Total size range in material examined: 1.07–1.80 mm.

Distribution.—Eastern North America, from southern Ontario and Quebec to southern Texas and Florida, east of the 100th meridian (see Fig. 26). About 850 specimens examined from the following localities: **CANADA**: ONTARIO: Fonthill, Marmora, Toronto; QUEBEC: Lanoraie, Montreal, St. Jean; **UNITED STATES**: ALABAMA: Mobile; ARKANSAS: Hope; CONNECTICUT: New Haven; FLORIDA: Archbold Biological Station, Enterprise, Highlands Hammock State Park (6 mi. W Sebring), Jacksonville, 16 mi. W Miami; GEORGIA: Cornelia, Savannah, St. Simons Is., Waycross; ILLINOIS: Antioch, Carterville, Chicago, Des Plaines, Fort Sheridan, Fox, Frankfort, Glen Ellen, Glenview, Mound City, Oakwood, Steger, White Heath; INDIANA: Dune Acres, Dune Park, Posey Co.; IOWA: Cedar Rapids, Iowa City; KANSAS: Topeka; KENTUCKY: Mammoth Cave National Park; LOUISIANA: 4 mi. S Grosse Tete, New Orleans; MARYLAND: Berwyn; MASSACHUSETTS: Boston, Belmont, Concord, Naushon Island, Springfield, Tewksbury; MICHIGAN: Genessee Co., Lapeer and Irish Rds. (Lapeer Co.); MISSOURI: St. Louis, Willard; NEBRASKA: no specific locality; NEW JERSEY: Alpine, Hackensack; NEW YORK: Buffalo, De Bruce, Hempstead, Ithaca, New York, Pike; NORTH CAROLINA: Raleigh; OHIO: Cincinnati; OKLAHOMA: 2 mi. N Atoka; PENNSYLVANIA: Allegheny, Easton, Germantown, Glen Olden, Haverford, Jeanette, Mt. Airy, Pittsburgh, Tinicum Is., Twin Lakes, West View; TENNESSEE: no specific locality; TEXAS: Harris Co., Lee Co., San Antonio, San Diego, Welder Wildlife Refuge (near Sinton); VERMONT: East Dorset, Manchester, Peru; VIRGINIA: no specific locality; WEST VIRGINIA: Fairmont; WISCONSIN: Beaver Dam, Delavan. [AMNH, ANSP, CAS, CIN, CM, CNC, CNHM, CU, INHS, JFC, JFL, JS, KU, MCZ, MNHN, UAL, UCD, USNM, UW.]

Host fungi.—*Ganoderma applanatum* [20(11)]; *Ganoderma zonatum* [2(1)]; *Polyporus hydnoides* [2(1)]; *Ganoderma lucidum* [1]; *Fomes sclerodermeus* [1]; *Fomes pinicola* [1].

Discussion.—This is a moderately short and broad species with 8-segmented antennae, and it most nearly resembles *C. similis*, *C. schaefferi*, and *C. punctulatus*. It differs from the first two species by having finer and sparser elytral punctation and may be distinguished from *C. punctulatus* by its finer and sparser pronotal punctation and slightly transverse abdominal pore in the male. *C. castaneipennis* is also somewhat similar to *sallei* but differs in the elytral punctation, which is single, coarse, and dense. Because of the similarity in color pattern, this species has often been confused with *C. punctulatus rubriculus*, with which it is broadly sympatric. Although there are some differences in the elytral coloration and the form of the pronotal

horns, only the pronotal punctation and the form of the abdominal pore can be used to consistently separate the two species.

The populations of *C. sallei* from parts of Florida consist of somewhat smaller individuals, but the differences are not great enough to warrant the recognition of a distinct subspecies.

Ceracis sallei is one of the more common species of this genus in eastern North America, and throughout most of its range it occurs on the fungus *Ganoderma applanatum*. In the northern parts of the continent, it is often associated with *Eridaulus levettei* (Casey) and the tenebrionid beetle *Bolitotherus cornutus* Panz. In the southern states it may occur with *Ceracis multipunctatus* and *C. punctulatus punctulatus*. The evolution of host specificity in *C. sallei* and *C. punctulatus* is discussed in the section on the latter species.

Ceracis schaefferi Dury
Fig. 14

Ceracis schaefferi Dury, 1917: 25. Type locality: "Brownsville, Texas." Holotype, ♂, Dury Coll., CIN.

Plesiotypes.— ♂ and ♀, TEXAS: Brownsville, H. S. Barber, coll., ex *Ganoderma pseudoboletus* [USNM].

Male.—Length 1.55 mm. Body 2.14 × as long as broad. Head and pronotum reddish; elytra reddish, grading into reddish brown anteriorly; ventral surfaces reddish brown; legs, antennal funicle, and palpi yellowish brown, antennal club brownish. Vertex with a moderately deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 8-segmented; segment III 3 × as long as IV. Pronotum 0.93 × as long as broad, widest at middle; sides subparallel; anterior edge weakly produced, forming a very short and broad, elevated, subtrapezoidal lamina, which is shallowly emarginate at apex; disc impressed anteriorly just behind lamina; surface distinctly granulate; punctures about 0.12 × as large as scutellar base and separated by 0.75 to 1.50 diameters. Elytra 1.24 × as long as broad and 1.30 × as long as pronotum; sides subparallel for three-fourths of their lengths and abruptly converging near apices; punctation dual and confused, coarser and much denser than pronotal punctation, the punctures usually separated by less than 0.50 diameter. Metasternum 0.59 × as long as wide; suture absent. Abdomen 0.76 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.35 × as long as body of sternite, distinctly margined, and located posterad of center.

Female.—Length 1.55 mm. Body 2.21 × as long as broad. Vertex somewhat flattened; frontoclypeal ridge simple. Pronotum 0.93 × as long as broad; anterior edge rounded. Elytra 1.22 × as long as broad and 1.48 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to blackish, usually reddish and often suffused with varying amount of black or brownish; elytra yellowish to blackish, usually reddish posteriorly and blackish anteriorly. Sides of pronotum more rounded in females and small males; in larger males distinctly parallel-sided. Pronotal lamina varies according to size, but it is always short, broad, and distinctly elevated. Size and dimensions vary as follows in a series of 14 ♂♂ and 14 ♀♀ from Brownsville, Texas: TLmm: ♂ 1.25–1.55 (1.45 ± 0.023), ♀ 1.20–1.57 (1.44 ± 0.023); TL/EW ♂ 2.12–2.26 (2.17 ± 0.011), ♀ 2.09–2.25 (2.16 ± 0.010); PL/PW ♂ 0.88–0.96 (0.92 ± 0.007), ♀ 0.90–0.96 (0.93 ± 0.005); EL/EW ♂ 1.24–1.33 (1.28 ± 0.007), ♀ 1.26–1.36 (1.30 ± 0.007); EL/PL ♂ 1.35–1.55 (1.45 ± 0.015), ♀ 1.42–1.56 (1.50 ± 0.010). Total size range in material examined: 1.15–1.65 mm.

Distribution.—Southern Texas and eastern Mexico (see Fig. 28). About 150 specimens examined from the following localities: **UNITED STATES**: TEXAS: Brownsville, Columbus; **MEXICO**: NUEVO LEON: 5 mi. S Monterrey; TAMAULIPAS: Tam-

pico; VERACRUZ: 3 mi. N Fortin. [CAS, CNC, JFL, MCZ, USNM.]

Host fungi.—*Ganoderma* sp. [1].

Discussion.—This is a short and broad, reddish species in which the elytral punctation is much coarser and denser than that of the pronotum. It resembles *C. sallei*, with which it is sympatric in southern Texas, but it is easily distinguished from that species by the elytral punctation and the short pronotal lamina in the male. It appears to be most closely related to *Ceracis similis*, but the latter is somewhat more elongate, with a more prominent pronotal lamina in the male.

Ceracis schaefferi is another tropical Mexican species, extending from southeastern Mexico into southern Texas. The only known host is an unidentified species of *Ganoderma*. The closely related *C. similis* occurs in western Mexico and Baja California and has been collected on species of *Ganoderma*; further collecting in Mexico may reveal that *C. schaefferi* is an eastern race of *similis*.

Ceracis singularis (Dury) NEW COMBINATION
Fig. 12

Xesto singularis Dury, 1917: 14. Type locality: "Cincinnati, Ohio." Types, Dury Coll., CIN. *Ceracis* sp. (in part), Graves, 1960: 66.

Plesiotypes.— ♂ and ♀, NORTH CAROLINA: 1 mi. SW Brevard, Transylvania Co., June 21, 1962. No. 150 R. C. Graves, ex *Polyporus gilvus* [MCZ].

Male.—Length 1.60 mm. Body 2.29 × as long as broad. Head and apex of pronotum reddish, remainder of pronotum dark reddish brown; elytra, prosternum, and abdomen reddish, pectus dark reddish brown; legs, antennal funicle, and palpi brownish yellow, antennal club dark brown. Vertex with a transverse impression, in the center of which is a deep, circular fovea; frontoclypeal ridge produced, forming a short, broad, slightly concave lamina, which is shallowly emarginate at apex. Antennae 10-segmented; segment III 1.25 × as long as IV. Pronotum 0.96 × as long as broad, widest behind middle; sides broadly rounded; anterior edge produced, forming a lamina which is deeply emarginate apically and bears a short, longitudinal elevation on each side, giving the appearance of 2 rounded, slightly divergent horns, each bearing a dorsal knob; disc impressed anteriorly between the 2 knobs; surface distinctly granulate; punctures about 0.10 × as large as scutellar base and separated by 1.0 to 2.0 diameters. Elytra 1.39 × as long as broad and 1.56 × as long as pronotum; sides subparallel for half of their lengths and gradually converging apically; punctation dual and distinctly seriate, the large punctures forming relatively straight rows; interstices convex, giving the appearance of several raised, longitudinal ridges. Metasternum 0.54 × as long as wide; suture barely indicated posteriorly. Abdomen 0.87 × as long as wide at base; sternite III with a transverse, median, setigerous pore, which is 0.71 × as long as wide, 0.23 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.52 mm. Body 2.18 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.92 × as long as broad, widest at posterior fifth; sides gradually converging apically; anterior edge rounded. Elytra 1.39 × as long as broad and 1.62 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually reddish or dark reddish brown with the apex reddish; elytra yellowish to black, usually reddish or dark reddish brown, commonly lighter in color than pronotum, occasionally with basal third blackish and apical two-thirds reddish. In smaller males, the anterior edge of the pronotum is weakly produced and shallowly emarginate, and the knobs are barely developed as short carinae. In larger specimens the horns are well developed and distinctly divergent and the knobs project well above the plane of the lamina. Pro-

notal punctation varies and may be somewhat coarser and denser than that described for the plesiotype. Size and dimensions vary as follows in a mixed series of 14 ♂♂ and 14 ♀♀ from North Carolina: TLmm: ♂ 1.45–1.82 (1.68 ± 0.037), ♀ 1.42–1.70 (1.57 ± 0.022); TL/EW ♂ 2.21–2.45 (2.33 ± 0.020), ♀ 2.14–2.33 (2.24 ± 0.016); PL PW ♂ 0.93–1.04 (0.99 ± 0.009), ♀ 0.89–1.00 (0.94 ± 0.008); EL/EW ♂ 1.34–1.47 (1.39 ± 0.011), ♀ 1.31–1.44 (1.38 ± 0.009); EL/PL ♂ 1.36–1.58 (1.48 ± 0.021), ♀ 1.52–1.68 (1.61 ± 0.010). Total size range in material examined: 1.30–2.00 mm.

Distribution.—Eastern North America, from northern Minnesota and Massachusetts to southeastern Texas and Louisiana, east of the 100th meridian; a single isolated record from Costa Rica (see Fig. 33). About 280 specimens have been examined from the following localities: **CANADA**: ONTARIO: Leamington; **UNITED STATES**: ALABAMA: Selma; ARKANSAS: southwest; DISTRICT OF COLUMBIA: Washington; ILLINOIS: Antioch, Des Plaines, Fox, Galesburg, Glen View, Normal, Pt. Chester, Quincy, White Heath; INDIANA: Evansville; KENTUCKY: Mammoth Cave National Park; LOUISIANA: Audubon State Park; MARYLAND: Edgewood, Plummer's Island; MASSACHUSETTS: Cummington, Naushon Island, Woods Hole; MICHIGAN: Detroit; MINNESOTA: 10 mi. E Detroit Lakes; MISSISSIPPI: 15 mi. N Ackerman; NEBRASKA: Central City; NEW YORK: Ithaca, St. Hubert's; NORTH CAROLINA: 1 mi. SW Brevard, 6 mi. SE Cashiers, Joyce Kilmer Forest, 1¼ mi. SE Lake Toxaway, Magnolia, Moore Co., 1 mi. S Oakland, Raleigh, Randolf Co., ¾ mi. SE Rocky Knob, Sampson City; OHIO: Cincinnati; OKLAHOMA: 2 mi. N Atoka; PENNSYLVANIA: Chestnut Hill, Wissahickon Cr.; SOUTH CAROLINA: Florence, Moncks Corners, Santee State Park, Yemassee; TENNESSEE: Cumberland Gap, Bledsoe State Forest; TEXAS: Huntsville; VIRGINIA: Clapham Junction; **CENTRAL AMERICA**: COSTA RICA: Irazu, 1500′. [AMNH, BMNH, CNC, CNHM, CU, INHS, JFC, JFL, MCZ, USNM.]

Host fungi.—*Polyporus gilvus* [12(4)]; *Ganoderma applanatum* [3(1)]; *Fomes robiniae* [2(1)]; *Poria nigra* [1(1)]; *Lenzites saepiaria* [1(1)]; *Ganoderma curtisii* [1]; *Fomes conchatus* [1]; *Fomes igniarius* [1]; *Trametes hispida* [1]; *Polyporus versicolor* [1]; *Polyporus pargamenus* [1].

Discussion.—This is easily distinguished from all other species of *Ceracis* by the 10-segmented antennae, distinctly seriate elytral punctation, and the very peculiar pronotal horns in the male. Each horn bears a distinct protuberance above, which is evident even in smaller males. The only species with similar horns is *C. furcicollis* (Blair) from Polynesia; although the antennae of *furcicollis* are 10-segmented, the elytral punctation is not seriate. Seriate elytral punctation also occurs in *C. pullulus*, but that species has 9-segmented antennae and different pronotal modifications.

Ceracis singularis has a rather peculiar distribution. It occurs throughout the eastern United States, being more common in the Midwest, and has also been collected on Mt. Irazu in Costa Rica. Its absence in Mexico may be an artifact of collecting, but it is also possible that the Costa Rican population is a southern relict. Host records indicate a strong preference for *Polyporus gilvus* and related fungi with reddish brown fruiting bodies. It is one of the few North American ciids to breed in the woody fruiting bodies of *Fomes robiniae*.

Ceracis thoracicornis (Ziegler) NEW COMBINATION

Fig. 21

Cis thoracicornis Ziegler, 1845: 270. Type locality: "Carolina." Types?, LeConte Coll., MCZ.

Eucanthron thoracicorne. — LeConte, 1867: 58; Casey, 1898: 88; Blatchley, 1910: 900; Dury, 1917: 23, 24; Weiss and West, 1920: 8; Weiss and West, 1921: 169; Boving and Craighead, 1931: 270–271, pl. 92, fig. R (larva).

Eucanthron mellii Mellié, 1848: 369; Casey,

1898: 88 (syn.). Type locality: "Amerique boreale." Holotype, ♂, Melly Coll., GEN.

Cis pumicatus Mellié, 1848: 333, pl. 11, fig. 11. Type locality: "Nouvelle-Orleans." Holotype, ♀, Pic Coll. (Chevrolat Coll.), MNHN. NEW SYNONYMY.

Octotemnus ? pumicatus (Mellié), Casey, 1898: 91.

Ennearthron unicolor Casey, 1884: 37; Casey, 1898: 88 (syn.). Type locality: "Willet's Point, Long Island" [New York]. Holotype, ♂, Casey Coll., USNM.

Ennearthron laminifrons Casey, 1898: 89; Dury, 1917: 24. Type locality: "Louisiana (Morgan City)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Ennearthron piceum Casey, 1898: 88; Dury, 1917: 24. Type locality: "Texas (Columbus)." Holotype, ♂, Casey Coll., USNM. NEW SYNONYMY.

Ennearthron oblongus Blatchley, 1910: 900; Dury, 1917: 24; Weiss and West, 1920: 8. Type locality: "Marion Co." [Indiana]. Types, Blatchley Coll., PURD. NEW SYNONYMY.

Cis thoracicus Dalla Torre, 1911: 19. Incorrect subsequent spelling.

Ceracis bifoveatus Dury, 1917: 26. Type locality: "Cincinnati, Ohio." Holotype, ♂, Dury Coll., CIN. NEW SYNONYMY.

Cis thoracicinus Sherborn, 1931: 6493. Incorrect subsequent spelling.

Plesiotypes.— ♂ and ♀, VERMONT: East Dorset, Bennington Co., July 2, 1965, Lot 1768 J. F. Lawrence (C. Parsons, coll.), ex *Polyporus pargamenus* [MCZ].

Male.—Length 1.55 mm. Body 2.38 × as long as broad. Head and apex of pronotum reddish brown; remainder of pronotum, ventral surfaces, and greater portion of elytra black, a median elytral fascia, extending along the suture and widening apically, reddish; legs, antennal funicle, and palpi yellowish brown, antennal club dark brown. Vertex with a deep, transverse impression, preceded by a median elevation; frontoclypeal ridge produced, forming a relatively long, slightly concave, elevated, trapezoidal lamina, which is shallowly emarginate at apex. Antennae 9-segmented; segment III 1.67 × as long as IV. Pronotum 1.04 × as long as broad, widest at middle; sides subparallel; anterior edge strongly produced and deeply emarginate, forming 2 approximate, diverging horns, which are circular in cross-section and narrowly rounded at apices; disc impressed anteriorly just behind the horns and bearing a short, transverse carina laterad of each; surface distinctly granulate; punctures about 0.14 × as large as scutellar base and separated by 1.0 to 1.5 diameters. Elytra 1.38 × as long as broad and 1.38 × as long as pronotum; sides very weakly rounded, diverging to about middle and converging posteriorly; punctation dual and confused, finer and sparser than pronotal punctation posteriorly, becoming coarser and denser anteriorly. Metasternum 0.52 × as long as wide; suture barely indicated posteriorly. Abdomen 0.86 × as long as wide at base; sternite III with a circular, median, setigerous pore, which is 0.30 × as long as body of sternite, indistinctly margined, and located posterad of center.

Female.—Length 1.40 mm. Body 2.33 × as long as broad. Vertex slightly convex; frontoclypeal ridge simple. Pronotum 0.95 × as long as broad; anterior edge rounded. Elytra 1.50 × as long as broad and 1.80 × as long as pronotum. Sternite III without a setigerous pore.

Variation.—Color of pronotum yellowish orange to black, usually dark reddish brown or blackish, with apex commonly reddish brown; elytra yellowish to black, usually dark reddish brown or black and almost always with some reddish pigment along the suture posteriorly. Surface of pronotum very lightly to distinctly granulate, so that it may appear shiny or dull. Pronotal punctures vary somewhat in size and density. Frontoclypeal ridge in smaller males short and broad; elongate and trapezoidal in larger specimens. Pronotum usually narrower and more rounded in smaller males and the anterior edge only slightly produced, forming 2 small tubercles; in larger individuals the pronotum is broader and more parallel-sided and the anterior edge bears 2 long diverging horns. Size and dimensions vary as follows in a series of 14 ♂♂ and 14 ♀♀ from Bennington Co., Vermont (Lots 1719, 1730, and 1768): TLmm.: ♂ 1.10–1.55 (1.40 ± 0.033), ♀ 1.10–1.45 (1.33 ± 0.025);

TL/EW ♂ 2.26–2.50 (2.38 ± 0.020), ♀ 2.22–2.37 (2.29 ± 0.011); PL/PW ♂ 0.94–1.09 (1.02 ± 0.013), ♀ 0.91–1.00 (0.94 ± 0.006); EL/EW ♂ 1.36–1.50 (1.42 ± 0.012), ♀ 1.39–1.54 (1.46 ± 0.010); EL/PL ♂ 1.38–1.60 (1.49 ± 0.017), ♀ 1.67–1.90 (1.76 ± 0.017). Total size range in material examined: 1.00–1.67 mm.

Distribution.—Eastern North America, from southeastern Manitoba and southern Quebec to southern Texas and Florida, east of the 100th meridian (see Fig. 31). About 1300 specimens examined from the following localities: **CANADA**: MANITOBA: Aweme, Falcon Lake, Victoria Beach; ONTARIO: Leamington, St. Thomas, Toronto; QUEBEC: Montmorency Co., Montreal Is., Terrebonne Co.; **UNITED STATES**: ALABAMA: 6 mi. SE Eutaw, Mobile; ARKANSAS: Washington Co.; CONNECTICUT: New Haven, Stamford; DISTRICT OF COLUMBIA: Takoma Park, Washington; FLORIDA: Chipola Park (Dead Lake), 4 mi. NW Copeland, Dunedin, Enterprise, Highlands Hammock State Park (6 mi. W Sebring), Kissimmee, Lake Annie, 2.5 mi. SE Lake City, Palatka, St. Petersburg; GEORGIA: Valdosta, 12 mi. SSE Valdosta; ILLINOIS: Exeter, Fort Sheridan, Fox, Karnak, Oakwood, Olive Branch, St. Clair Co., Springfield, Steger, Urbana, West Pullman, White Heath, Willow Springs; INDIANA: Beverly Shores, Dune Acres, Marion Co., Mt. Vernon, Shelby; IOWA: Ames, Cedar Rapids, Estherville, Gutenburg; KANSAS: Benedict, Lawrence, Onaga, Topeka, Winfield; KENTUCKY: Mammoth Cave National Park; LOUISIANA: Audubon State Park, Baton Rouge, Fontainebleau State Park, Harahan, Killian, Lewiston, 5 mi. S Livingston, Morgan City, New Orleans, Norco, 14 mi. W Port Allen, Tallulah; MAINE: Monmouth, Paris, Weld; MARYLAND: Baltimore, College Park, 2 mi. E Silver Springs, Sparrows Point; MASSACHUSETTS: Arlington Heights, Belmont, Boston, Cambridge, Concord, Dracut, Framingham, Petersham, 2 mi. S Plymouth, Naushon Is., 10 mi. SE North Adams, Sherborn, Stoneham, Swansea; MICHIGAN: Detroit, Douglas Lake, Lansing, Lapeer State Game Area, Richfield Center, Whitmore Lake, 15 mi. SE Saugatuck; MINNESOTA: Cormorant, Lake Minnetonka, Mille Lacs Lake, Olmstead Co., Winnebago Creek Valley; MISSISSIPPI: 15 mi. N Ackerman, Little Mountain Park, N. Augusta, 4 mi. W Starkville; MISSOURI: Kansas City; NEBRASKA: Central City; NEW HAMPSHIRE: Farmington, Squam Lake, 7 mi. NW Wilton; NEW JERSEY: Atlantic Co., Mercer Co., Middlebush, Middlesex Co., Monmouth Junction, Oakland, Springfield, Fort Lee; NEW YORK: Albany, Flushing (Long Island), Hamburg, Ithaca, Lancaster, New York, Niagara, N. Fairhaven, Olcott, St. Hubert's, Staten Island, West Point; NORTH CAROLINA: 1 mi. SW Brevard, Calypso, 6 mi. SE Cashiers, 3 mi. W Highlands, 4 mi. W Highlands, Magnolia, Moore Co., 1 mi. S Oakland, 1 mi. E Oakland, 3 mi. SSW Oakland, 4 mi. SSW Oakland, 4 mi. S Oakland, Raleigh; OHIO: Cincinnati, Columbiana, E. Liverpool; PENNSYLVANIA: Allegheny, Chestnut Hill, Clinton, Easton, Jeannette, Philadelphia, Pittsburgh, Twin Lakes, Wissahickon Creek; RHODE ISLAND: Berkeley; SOUTH CAROLINA: Moncks Corners, Santee State Park, Walterboro, Yemassee; TENNESSEE: Memphis; TEXAS: Brownsville, Columbia, Columbus, Dennison, Nachadoches, Victoria; VERMONT: East Dorset, Manchester, Peru; VIRGINIA: Chain Bridge, Clapham Junction, Falls Church, Fredericksburg, Vienna; WISCONSIN: Beaver Dam, Powers Lake. [AMNH, ANSP, CAS, CIN, CM, CNC, CNHM, CU, HH, INHS, JFC, JFL, JS, KU, MCZ, MNHN, PURD, UAL, UAZ, UCD, USNM.] A series of specimens apparently collected in San Luis Obispo Co., California, have almost certainly been mislabeled.

Host fungi.—*Polyporus pargamenus* [31 (10)]; *Polyporus adustus* [11(4)]; *Polyporus supinus* [9(5)]; *Polyporus versicolor* [9(1)];

Lenzites betulina [8(2)]; *Polyporus sector* [5 (1)]; *Daedalea ambigua* [4(2)]; *Daedalea unicolor* [4(2)]; *Polyporus gilvus* [4]; *Ganoderma lucidum* [3(1)]; *Ganoderma applanatum* [3]; *Ganoderma tsugae* [3]; *Trametes corrugata* [2(1)]; *Polyporus abietinus* [1 (1)]; *Polyporus spraguei* [1(1)]; *Trametes hispida* [1(1)]; *Ganoderma* sp. [1(1)]; *Polyporus squamosus* [1]; *Polyporus hydnoides* [1]; *Polyporus fumosus* [1]; *Polyporus sulphureus* [1]; *Fomes fomentarius* [1]; *Fomes pinicola* [1]; *Boletus* sp. [1].

Discussion.—This is a moderately small, dark colored species with relatively fine and sparse punctation, 9-segmented antennae, and 2 narrow, diverging pronotal horns in the male. It is probably most closely related to the Neotropical species *C. cucullatus* and *C. bicornis*, from which it differs by the somewhat coarser pronotal punctation and different pronotal modifications. It is similar in size and form to *C. pullulus*, which has seriate elytral punctation and a rounded, emarginate pronotal lamina in the male. Smaller specimens resemble *C. minutus* and *C. minutissimus*, both of which have 8-segmented antennae. *C. quadricornis* has similar coloration and pronotal horns, but the antennae are 8-segmented and the elytra are much narrower. The species also resembles the western *C. californicus*, which is somewhat more elongate and has much coarser and denser elytral punctation.

Like *C. californicus*, this species is quite variable, not only in size, but in the form of pronotum and elytra, pronotal horns in the male, and pronotal punctation. As a result several names have been applied to it. The more typical eastern form was described as *Cis thoracicornis* by Ziegler (1845), *Ennearthron mellyi* by Mellié (1848), and *Ennearthron unicolor* by Casey (1898). Mellié also gave the name *Cis pumicatus* to a single female from New Orleans. Casey (1898) considered *unicolor* and *mellyi* to be synonymous with *thoracicornis*, and he described two more species, *Ennearthron piceum* and *E. laminifrons*. *E. piceum* from Texas and Louisiana was described as having the prothorax impressed behind the horns, and *E. laminifrons* from Louisiana was distinguished by having shorter elytra. Blatchley (1910) described *Ennearthron oblongus* from Indiana, which was said to differ from *thoracicornis* by having coarser pronotal punctation. Finally, Dury (1917) proposed the name *Ceracis bifoveatus* for a series from Cincinnati with 8-segmented antennae and peculiar modifications of the 3rd abdominal sternite in the male. The types of all of these species have been examined, and they are all considered to be variants of *C. thoracicornis*. The segments were miscounted in *C. bifoveatus*, and the slight depression in front of the male abdominal pore also occurs in some *thoracicornis*. Some of the above species names refer to geographic variants, but I do not think that there are any clearly recognizable subspecies. Northern populations seem to have coarser pronotal punctation than those in the south, and in southern populations the size may be smaller and the pronotal horns longer. The color pattern is relatively consistent throughout the range, and in mature adults it may be useful as a diagnostic character. The elytra are usually blackish, as is the pronotum, but there is usually a narrow reddish patch along the posterior part of the elytral suture.

Ceracis thoracicornis is the most common, widespread, and polyphagous species in eastern North America. It is fairly common in the northern states, and it extends into the southern parts of Manitoba, Ontario, and Quebec. It has been collected on 24 different species of fungi and apparently breeds in at least 14 of these. Its preferred host appears to be *Polyporus pargamenus*, with 31 records and 10 of these breeding records, but it is also quite common on *P. adustus*, *P. supinus*, and members of the *Polyporus versicolor* group. In the northern part of its range it occurs with *Cis confusus* Blatchley, *Cis horridulus* Casey, and *Cis striolatus* Casey on *P. pargamenus*, and with *Cis fuscipes* Mellié, *Cis pistoria* Casey, *Sulcacis lengi* Dury, *Strigocis opacicollis* Dury,

and *Octotemnus laevis* Casey on *P. versicolor* and its relatives. All of these associated species are northern Holarctic forms with relatives in Europe and Asia, while *C. thoracicornis* and all other known North American *Ceracis* have affinities with Neotropical species. In the southern part of the range, the species has more of a tendency to be polyphagous, and is fairly common on *Polyporus supinus*, *P. sector*, and *Daedalea ambigua*.

This species, like *C. californicus*, breeds in fungi falling into both of Paviour-Smith's host preference groups, *P. adustus* and *Ganoderma lucidum* (among others) belonging to one group and *P. versicolor*, *Lenzites betulina* and several others belonging to the second group. My own records for North American ciids indicate that *P. pargamenus*, *P. sector*, and *P. abietinus* form a third group, for which *C. thoracicornis* is both an indicator and an exception. The absence of any close relatives in North America may partly explain the broad host range of this species.

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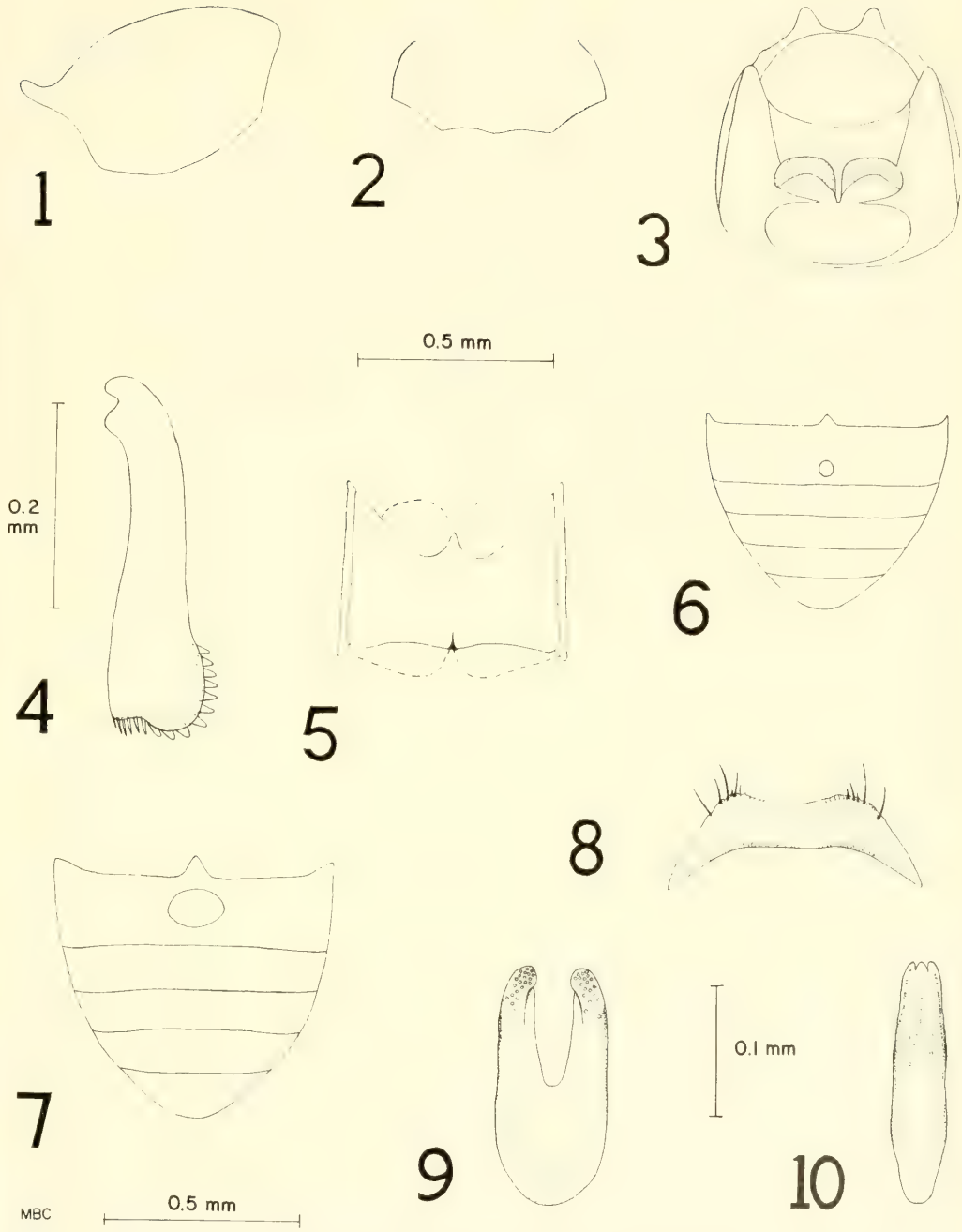
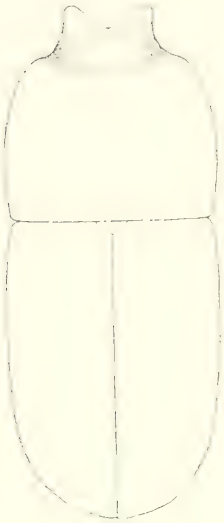


Figures 1–5. *Ceracis sallei* Mellié. Fig. 1. Pronotal disc, lateral view. Fig. 2. Cross-section of prosternum (anterad of intercoxal process). Fig. 3. Prothorax, ventral view. Fig. 4. Protibia, anterior view. Fig. 5. Metasternum, showing very short median suture. Fig. 6. *Ceracis punctulatus rubriculus*, n. ssp., male, abdomen, ventral view, showing small round setigerous pore. Fig. 7. *Ceracis obrieni*, n. sp., male, abdomen, ventdal view, showing large, transverse setigerous pore. Figures 8–10. *Ceracis sallei* Mellié, male. Fig. 8. Abdominal sternite VIII. Fig. 9. Tegmen, ventral view. Fig. 10. Median lobe, dorsal view.



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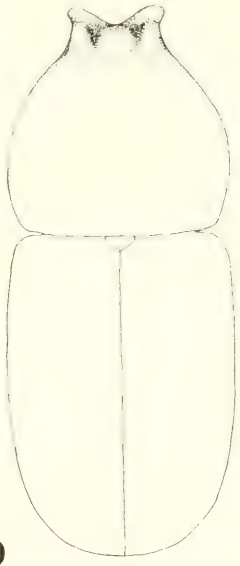

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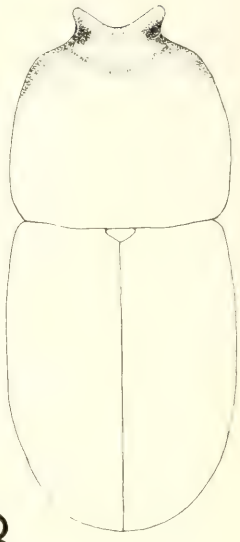

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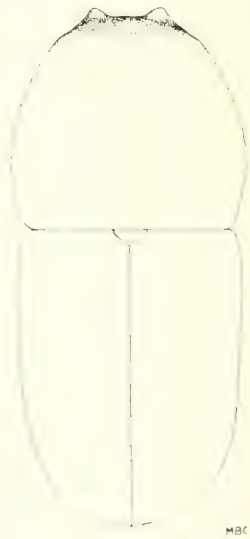

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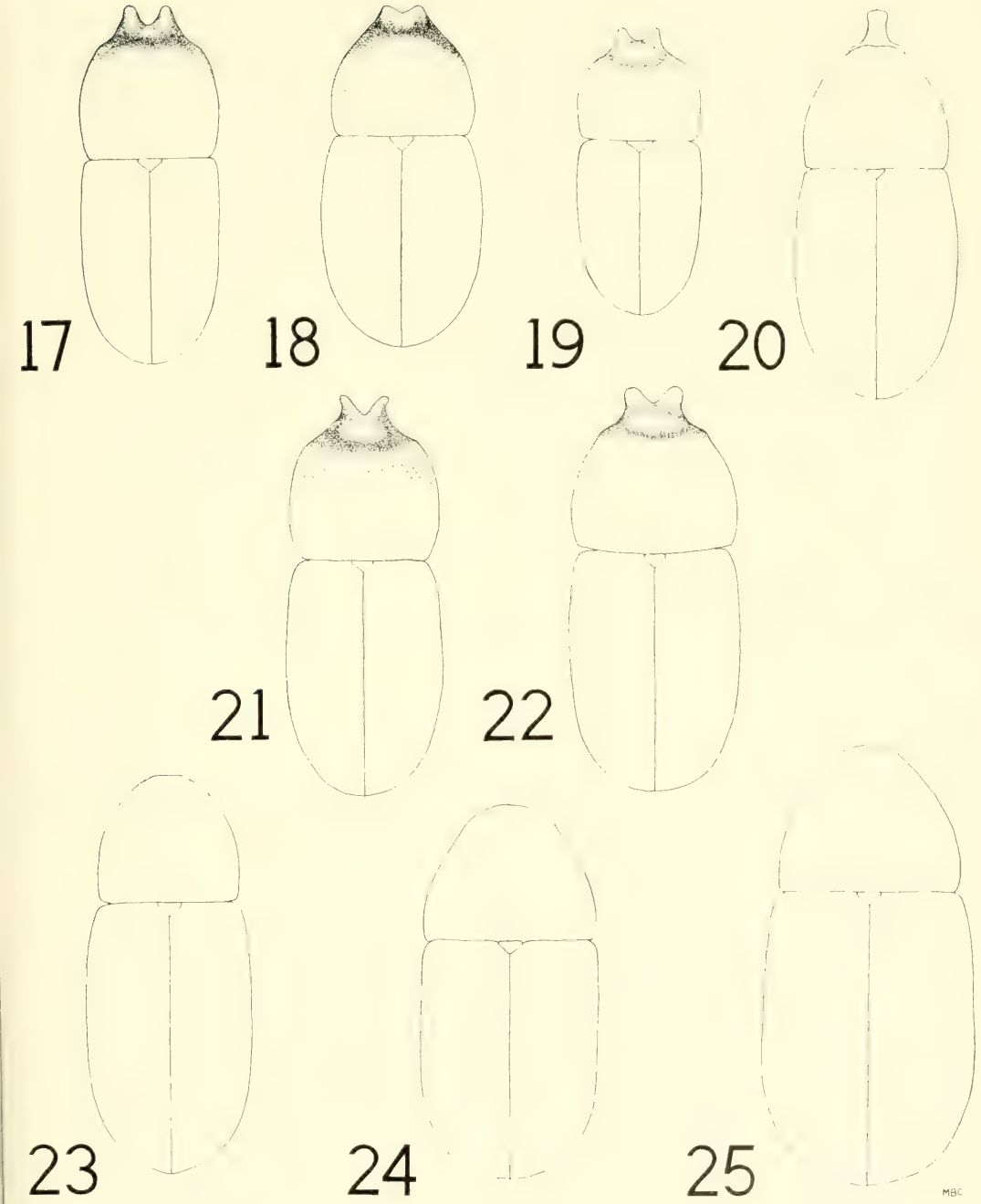
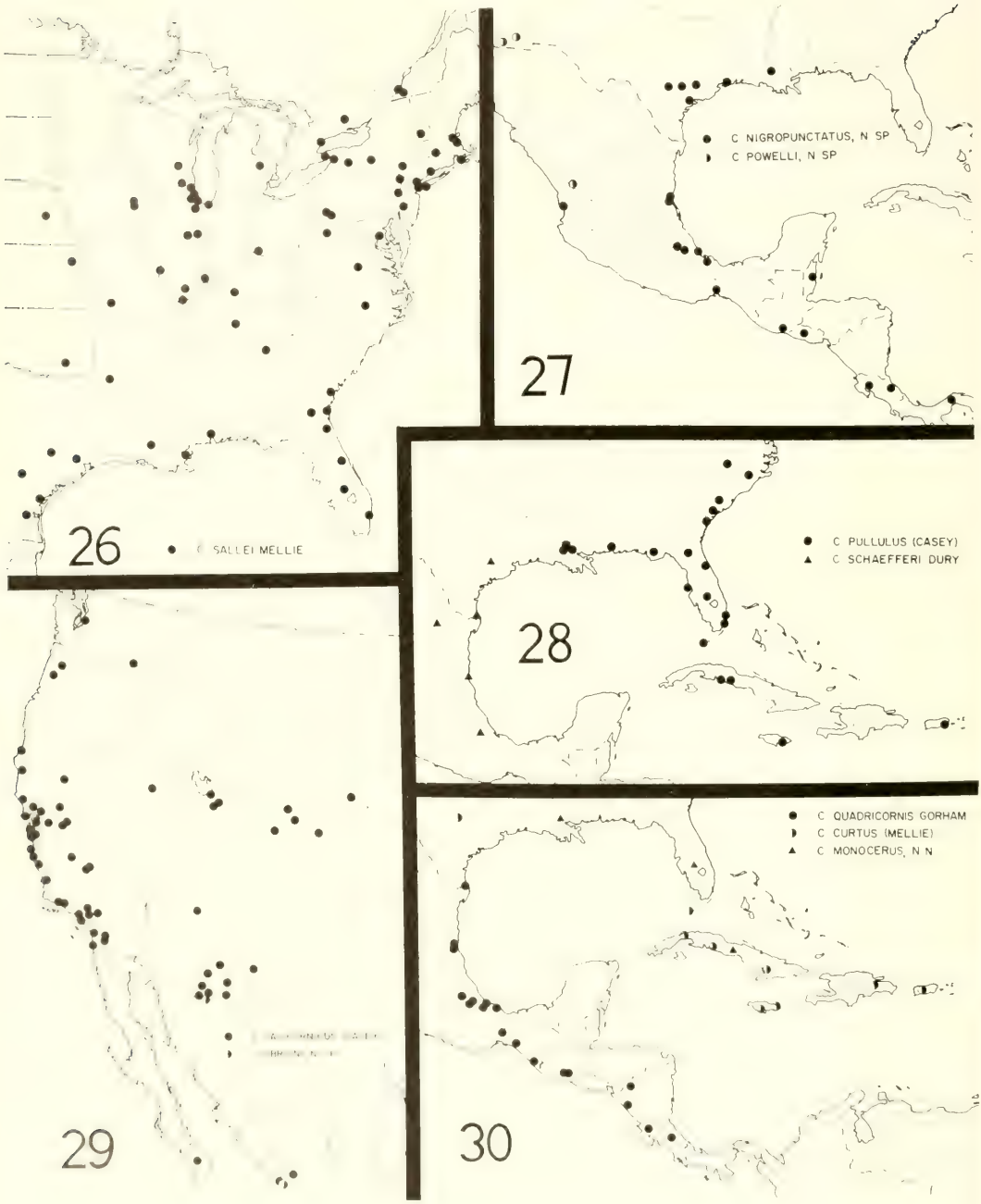
Figures 11–16. *Ceracis* spp., male, dorsal view. Fig. 11. *C. sallei* Mellié. Fig. 12. *C. singularis* (Dury). Fig. 13. *C. punctulatus rubriculus*, n. ssp. Fig. 14. *C. schaefferi* Dury. Fig. 15. *C. californicus* (Casey). Fig. 16. *C.* [illegible]. All figures drawn to same scale.



Figures 17–25. *Ceracis* spp., male, dorsal view. Fig. 17. *C. quadricornis* Gorham. Fig. 18. *C. minutissimus* (Mellié). Fig. 19. *C. minutus* Dury. Fig. 20. *C. monocerus* new name. Fig. 21. *C. thoracicornis* (Ziegler). Fig. 22. *C. pullulus* (Casey). Fig. 23. *C. powelli*, n. sp. Fig. 24. *C. multipunctatus* (Mellié). Fig. 25. *C. obrieni*, n. sp. All figures drawn to same scale.


C NIGROPUNCTATUS, N SP
C POWELLI, N SP
27
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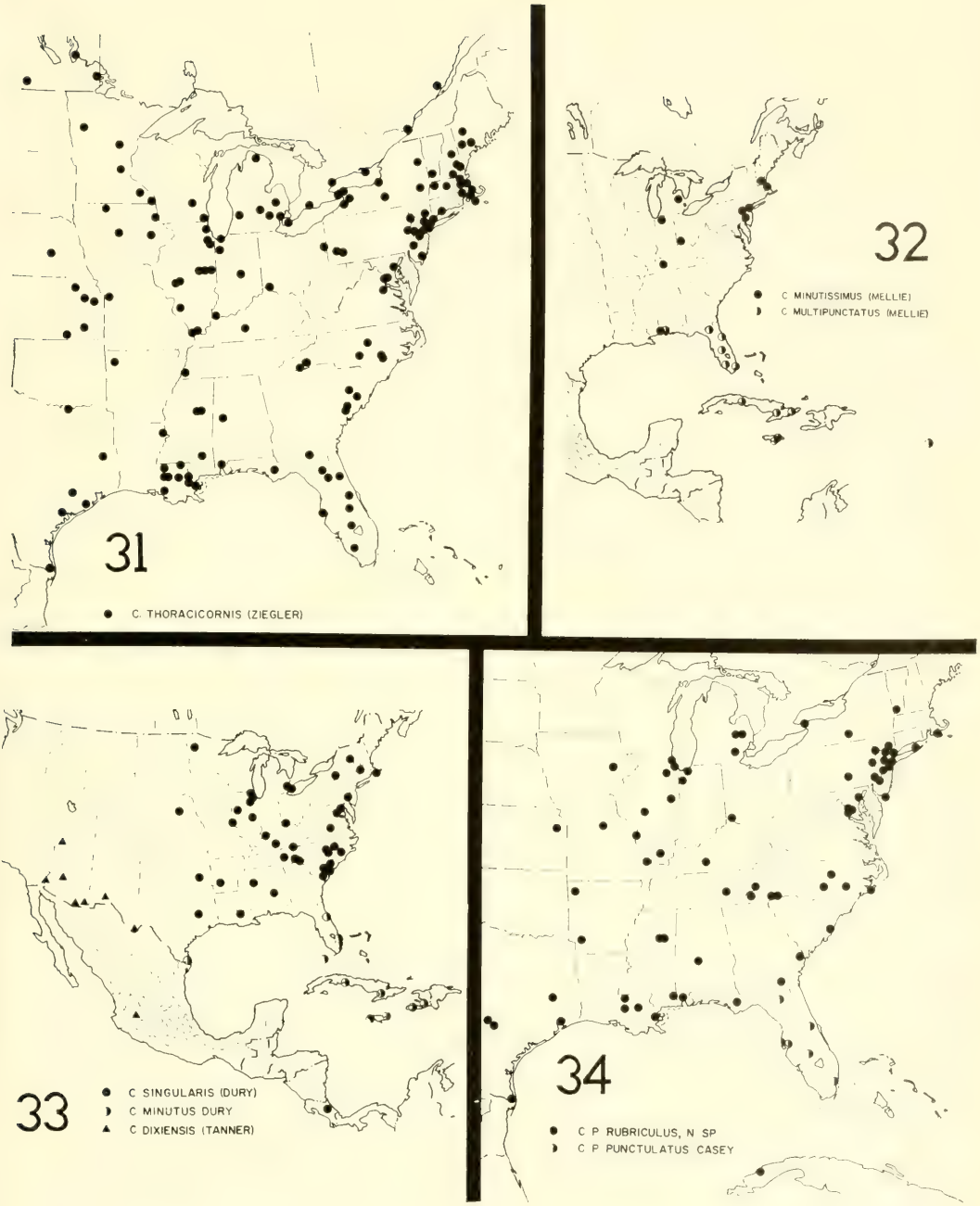
C SALLEI MELLIE
C PULLULUS (CASEY)
C SCHAEFFERI DURY
28
C QUADRICORNIS GORHAM
C CURTUS (MELLIE)
C MONOCERUS, N N
29
30


31
C. THORACICORNIS (ZIEGLER)
32
C. MINUTISSIMUS (MELLIE)
C. MULTIPUNCTATUS (MELLIE)
33
C. SINGULARIS (DURY)
C. MINUTUS DURY
C. DIXIENSIS (TANNER)
34
C. P. RUBRICULUS, N. SP.
C. P. PUNCTULATUS CASEY

Bulletin OF THE
Museum of
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Zoology

Systematics and Evolution of the Genus *Triodopsis* (Mollusca: Pulmonata: Polygyridae)

JOSEPH VAGVOLGYI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 7
FEBRUARY 12, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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JOSEPH VAGVOLGYI[1, 2]

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INTRODUCTION

The purpose of this work was to study the evolutionary biology of the genus *Triodopsis*. This is one of the most common genera of land snails in eastern North America, yet no comprehensive, modern work has been done on its systematics or evolution. Our knowledge concerning the group still comes mainly from the work of Pilsbry (1940) and Hubricht (1949; 1950a, b; 1952a, b; 1953; 1954; 1958). Perhaps it is permissible to say that, although valuable, these works are not based on modern conceptions of species, speciation, etc., but solely upon morphology. Thus it seemed that a restudy of the group was needed.

The results of this study are consistent with the tenets of the evolutionary theory. Of interest are the high frequency of hybridization and the rarity of clines. The new classification is both simpler and more consistent than the previous one.

Material was studied from various sources. Most important were the Museum of Comparative Zoology (MCZ) and the Academy of Natural Sciences of Philadelphia (ANSP). I also received some material from the Carnegie Museum of Pittsburgh (CM), the United States National Museum (USNM), and Mr. Leslie Hubricht, of Meridian, Mississippi. Finally, I obtained some material from my own field trips (JV). Four extensive collecting trips were made, each lasting eight to fifteen days, and several shorter ones. These covered an area extending from the Atlantic Coast to Illinois and Texas.

The following working methods were used. First, all the available samples of each species were surveyed. Then measurements of from three to eight characters were taken on representative samples from the various parts of the range, and the re-

[1] Science Department, Staten Island Community College, Staten Island, N.Y. 10301

[2] Published with the aid of a grant from the Committee on Evolutionary Biology of the Department of Biology, Harvard University.

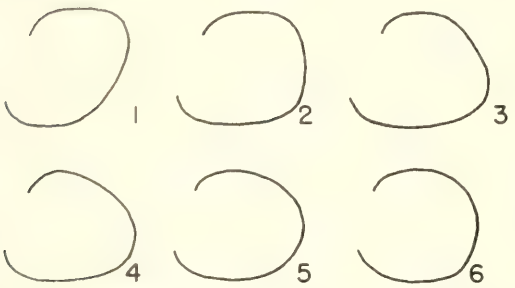


Figure 1. Aperture shape in *Triodopsis*. 1, Auriculate; 2, square; 3, trapezoid; 4, triangular; 5, oval; 6, circular.

sults obtained evaluated statistically. The distribution and ecology were then studied by plotting the records on large scale maps showing hydrography, vegetation, and elevation. Information on the distribution and ecology were also taken from the literature. In the last step, the data obtained from these various sources were synthesized.

Many of the terms used in this paper occur commonly in the literature, but some do not. Definitions of the necessary terms follow.

Aperture: the margin of the shell that surrounds the opening of the shell; also the surrounded area. The shape of the aperture may be auricular, square, trapezoid, triangular, oval, round, or intermediate between any of these (Fig. 1). These geometrical forms are actually never "complete," in the sense that the upper left corner is always truncated by the penultimate whorl. The term aperture is interchangeable with lip or peristome.

Aperture grade: the degree of development of the lip swelling, lip teeth and parietal lamella.

Armature: the lip teeth and the parietal lamella together.

Axis: the line drawn through the apex and the umbilicus of the shell.

Bifid: cleft into two lobes, e.g., a lip tooth.

Dished: concave, e.g., an aperture having the lip swelling and the lip teeth slanted inward.

Embryonic whorls: the first 1.4–1.5 whorls of the shell, produced by the embryo inside the egg.

Fulcrum: the callosity inside the last whorl, on the inner wall.

Granule: the small protuberance on the surface of the shell, which does not bear a hair. This term may be used synonymously with papilla; the latter, however, may bear a periostracal hair.

Height: the vertical distance between the lowest point of the aperture and the apex of the shell, measured with the axis held perpendicularly.

Keel: the ridge at the periphery of the whorl.

Lip: the margin of the shell, surrounding the opening of the shell; used synonymously with aperture or peristome. An upper and lower lip can be differentiated.

Lip swelling: the thickening at or near the lip. In the former case, it is marginal, in the latter, receding.

Lip tooth: the protrusion on the lip or lip swelling. It may be marginal or receding.

Lip tooth distance: the distance between the middle point of the tip of the lip tooth and the junction of the lip upon which the tooth rests with the shell.

Papilla: the small protuberance on the surface of the shell, which may bear a periostracal hair. Used synonymously with granule.

Peristome: the margin of the shell that surrounds the opening of the shell. Used synonymously with aperture and lip.

Scale: the small, flat projection of the periostracum.

Sculpture: the pattern of the surface of the shell—the hairs, scales, granules, etc.

Spiral direction: parallel with the direction of the coiling of the shell.

Transverse direction: perpendicular to the direction of the coiling of the shell.

Umbilicus: the opening at the base of the shell, resulting from a loosely coiled columella. Its diameter (width) is measured at the depth of the last whorl. The word umbilicus may stand for the longer term "width of the umbilicus."

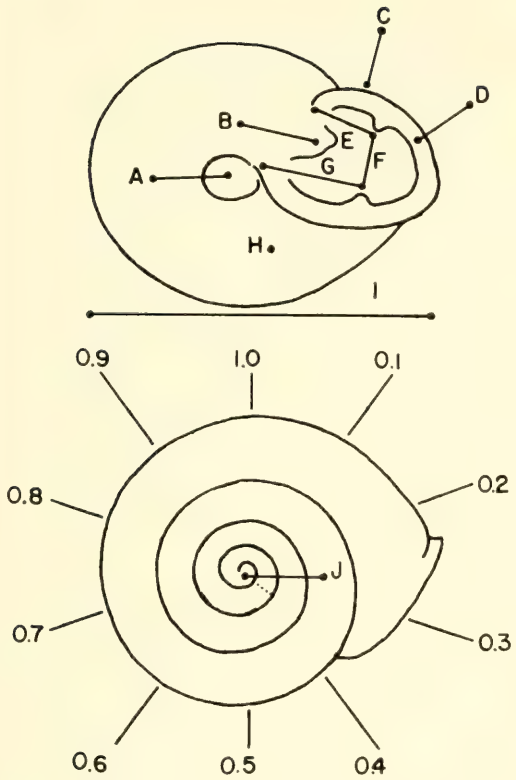


Figure 2. The more important features and measurements of the *Triodopsis* shell. *Above:* figure in side view. A, umbilicus; B, parietal lamella; C, lip, or aperture; D, lip swelling; E, upper lip tooth distance; F, distance between upper and lower lip teeth; G, lower lip tooth distance; H, last whorl; I, width of shell. *Below:* shell in top view. J, embryonic shell, 1.4 whorls. Numbers refer to whorl number; the shell shown has 4.4 whorls.

Whorl: the convolution of the shell. The number of whorls was measured under a binocular microscope, using a circular scale divided into ten parts, with the apex of the shell placed in the center of the circle.

Width: the greatest diameter of the shell across the last whorl. It is approximately perpendicular to the axis of the shell.

Wrinkle: the slight folding of the periostracum; longer than the granule, shorter and slighter than the stria.

The more important terms and measurements are figured below (Fig. 2).

ACKNOWLEDGMENTS

I wish to express my thanks to Dr. William J. Clench and Dr. R. Tucker Abbott for making the extensive collections of the MCZ and ANSP available for study. I also wish to thank Mr. Leslie Hubricht, Dr. J. P. E. Morrison and Dr. J. Parodiz for helping me with study material, and Mr. Wayne F. Grimm for furnishing information on the reproduction of *Triodopsis fallax*. I am most deeply indebted, however, to Dr. Ernst Mayr and Dr. Ruth D. Turner, who read and criticized the manuscript and made many helpful suggestions. Financial help was obtained from the Wenner-Gren Foundation, the Biological Laboratories of Harvard University, and the Society of Sigma Xi. I thank all of them sincerely.

A less elaborate version of this paper was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology, to the Department of Biology, Harvard University. Further work was done while the author was a Postdoctoral Research Fellow in Evolutionary Biology at Harvard University.

SYSTEMATIC TREATMENT

Order STYLOMMATOPHORA
Family POLYGYRIDAE
Genus TRIODOPSIS

Type species *Triodopsis lunula* Rafinesque = *Helix tridentata* Say[1]

Triodopsis Rafinesque, 1819, J. Phys. Chim. Hist. Nat. 88: 425.

Menomphis Rafinesque, 1831, Enumeration and account of some remarkable natural objects in the cabinets of Prof. Rafinesque, in Philadelphia, November 1831: 3. Subgenus of *Triodopsis* for *Triodopsis lunula* Rafinesque.

Triodontopsis Agassiz, 1846, Nomenclature Zool., Index Universalis: 378 (emendation of *Triodopsis*).

[1] Rafinesque listed *T. lunula* as the number one species when he described the genus *Triodopsis*. Férussac, 1821, Tabl. Syst. Fam. Limaçons, p. 34, no. 105, put *T. lunula* in the synonymy of *Helix tridentata* Say.

The genus *Triodopsis* belongs to the family Polygyridae, suborder Sigmurethra, order Stylommatophora (Pilsbry, 1940; Zilch, 1960). Its distinguishing features are mainly in the morphology of the reproductive organs. The penis is enveloped by a thin, membranous sheath, which is attached to the penis at the base. There is no stimulator in the penis, or flagellum on it, except for a vestigial flagellum in the subgenus *Cryptomastix*. The shells are small to moderately large, the aperture usually bears two teeth and a lamella; hence the scientific name *Triodopsis* (three-toothed face).

Twenty-two species belong to the genus. Of these, eighteen occur in eastern, and four in western North America. They live in various types of deciduous and mixed pine-deciduous forests, hiding in the litter layer under logs, branches or stones. A few species also occur in the grasslands. The majority of the species prefer the lower elevations, below 1500 feet, but a few may live over 3000 feet. Their food consists of dead leaves or fungi that live on the decaying plant material. The snails are active from early spring to late fall, the cycle being interrupted by temporary aestivations in time of drought. Their life span is several years. In the early spring they lay small batches of eggs a few centimeters below the surface of the ground. The number of eggs in a batch varies from two to twenty, their size, depending upon the species, from two to three and one-half millimeters. At room temperature they hatch in about three weeks. Some of the young grow fast, and reach maturity by the fall, others winter as young and complete their growth the next spring. The latter observations were made in the laboratory, and the possibility exists that the development of the young was slower than in nature. Cleave and Foster (1937) made similar observations on the related form *Mesodon thyroidus* (Say). Grimm, however, stated in a letter that he obtained two generations a year in *Triodopsis fallax*.

The genus is divided into four subgenera: *Triodopsis* (*sensu stricto*), *Xolotrema*, *Neohelix* and *Cryptomastix*. The first three subgenera lack an epiphallus and flagellum, and have only one pilaster in the cavity of the penis; the fourth, *Cryptomastix*, has an epiphallus, flagellum (vestigial), and two pilasters. The first three occur in the eastern parts of the United States and Canada; the fourth is confined to the northwestern United States and Canada. On these grounds, *Cryptomastix* might be considered a separate genus. Because of the subjective nature of classification on supraspecific levels, however, the current generic and subgeneric classification was adopted without any change. My work was oriented toward the specific and intraspecific problems, rather than a generic rearrangement.

The fossil remains of the genus are very scanty. Only a few Pleistocene records are known (Baker, 1920, 1928, 1937; Henderson, 1935; Hubricht, 1961; Leonard, 1952, 1953; Leonard and Frye, 1960; Shimek, 1936). The records include *Triodopsis juxtidens discoidea, T. neglecta vulgata, T. obstricta obstricta, T. o. denotata, T. fosteri fosteri, T. f. hubrichti, T. albolabris* and *T. multilineata*. These are identical or almost identical with the Recent forms. On this basis, it seems probable that most of the species are of Pleistocene or possibly Pliocene origin, and the "young" species developed in the late Pleistocene or Holocene.

Key to Species and Subspecies

The following key can be used to identify adult specimens of *Triodopsis*, except for intergrades. In order to increase its usefulness, dubious cases are keyed out twice. Thus, *T. c. complanata*, which may have small lip teeth or almost none, is keyed out among both the tooth-bearing and the toothless forms.

1a Shell umbilicated 2
b Shell imperforate 28
2a Embryonic shell smooth or striated; eastern United States 3
b Embryonic shell with striae and often also with granules; Pacific Coast 24

3a Umbilicus very narrow and partially covered by reflected edge of peristome 4
b Umbilicus narrow to wide, not covered by reflected edge of peristome 5
4a Shell width 17–26 mm, sculpture of triangular scales; lower lip swelling reaches columella; hybridizes with *o. obstricta*; from Vermont to Michigan and Tennessee *o. denotata*, p. 206
b Shell width 10–11 mm; no triangular scales; lower lip swelling terminates shortly before columella; restricted to North Carolina *soelneri*, p. 204
5a Lip teeth absent 6
b Lip teeth present 9
6a Aperture auricular, lip swelling thin, peristome sharp; intergrades with *f. obsoleta*, grade B; lower areas of the southeastern Coastal Plain, from Maryland to Georgia *f. obsoleta*, grade A, p. 187
b Aperture oval-triangular, lip swelling thin or thick, peristome swollen, at least in some places 7
7a Shell width 9–13 mm; Piedmont region of Virginia *burchi*, p. 160
b Shell width 17–27 mm 8
8a Shell width 26–27 mm, umbilicus very wide all the way; restricted to northern West Virginia *c. platysayoides*, p. 159
b Shell width 17–24 mm, umbilicus somewhat narrower at the early whorls and widens out later; Kentucky, Tennessee, and adjoining regions *c. complanata*, p. 157
9a Parietal lamella points at or below upper lip tooth when looking at the shell from below 10
b Parietal lamella points above upper lip tooth when looking at the shell from below 11
10a Lip swelling slightly receding, peristome sharp and flat; lip teeth moderate to large; from Ontario to Michigan, Georgia and Alabama *tridentata*, p. 151
b Lip swelling marginal, lip swollen, lip teeth usually small or lacking; *burchi* or *complanata*, go back to 7
11a Upper lip swelling slants inward, parietal lamella often very large; these features may not be clear, however; check description and figures of *rugosa* and *fulciden* 12
b Upper lip swelling does not slant inward, parietal lamella rarely large 13
12a Shell width 10–16 mm; West Virginia and neighboring areas *rugosa*, p. 161
b Shell width 8–9 mm; confined to the Piedmont region of North Carolina *fulciden*, p. 164
13a Upper lip tooth distance roughly the same as lower lip tooth distance 14
b Upper lip tooth distance is considerably greater than lower lip tooth distance 16
14a Shell and aperture depressed, umbilicus moderately wide, shell often smooth and shiny; Ohio and Mississippi valleys, from Ohio to Missouri *j. discoidea*, p. 171
b Shell and aperture not depressed, umbilicus narrow or very narrow, shell never smooth and shiny 15
15a Umbilicus narrower, coiling of shell tighter and parietal lamella larger; hybridizes with *j. juxtidens*; New Jersey and adjoining Pennsylvania and New York, also Virginia *j. stenomphala*, p. 169
b Umbilicus wider, coiling of shell looser and parietal lamella smaller; hybridizes with *j. stenomphala*; eastern seaboard from Vermont to Georgia, west to West Virginia *j. juxtidens*, p. 165
16a Lip teeth and parietal lamella large, and thus obstruct the aperture to a considerable degree 17
b Lip teeth and parietal lamella small or moderately large, and thus do not obstruct the aperture significantly 19
17a Fulcrum present, umbilicus narrow but suddenly widening at the last whorl 18
b Fulcrum absent, umbilicus wide; Appalachian Mountains in West Virginia and Virginia *fraudulenta*, p. 181
18a Lip swelling marginal, peristome swollen; hybridizes with *c. cragini*; Texas *c. copei*, p. 199
b Lip swelling slightly receding, peristome sharp; intergrades with *f. obsoleta* and *f. alabamensis*; Blue Ridge Mountains, and the higher regions of the southeastern coastal plain, from Pennsylvania to Georgia and Tennessee *f. fallax*, p. 184
19a Umbilicus wide 20
b Umbilicus narrow or medium wide, or narrow at the beginning and widening suddenly at the last whorl 21
20a Shell width 12–20 mm, coiling of shell moderately tight, umbilicus wide; intergrades with *n. neglecta*; from Ontario to Wisconsin, North Carolina and Tennessee *n. vulgata*, p. 175
b Shell width 10–13 mm, coiling very tight; intergrades with *n. vulgata*; Ozark area *n. neglecta*, p. 178
21a Last whorl, measured behind the aperture, is more than one and one-half times wider than the penultimate one, when looking at the shell from above;

lower lip tooth located close to columella; isolated spots in North Carolina, Pennsylvania and Ohio ..... *pendula*, p. 180

b Last whorl less than one and one-half times wider than the penultimate one, lower lip tooth near middle of lower lip 22

22a Aperture auriculate, peristome sharp, whorl-width ratio 0.39–0.53; intergrades with *f. obsoleta*, grade A, and *f. fallax*; hybridizes with *f. alabamensis*; southeastern Coastal Plain from Maryland to Georgia ..... *f. obsoleta*, grade B, p. 187

b Aperture square to oval, peristome often swollen, whorl-width ratio 0.47–0.68 23

23a Shell width 8–13 mm, number of whorls 4.9–7.0, upper lip tooth slightly receding; extensively hybridizes with *f. fallax* and *f. obsoleta*; Alabama, and an isolated spot in Virginia ..... *f. alabamensis*, p. 193

b Shell width 7–11 mm, number of whorls 4.3–5.5, upper lip tooth definitely receding; hybridizes with *c. copei*; from eastern Kansas to Texas and Louisiana ..... *c. cragini*, p. 201

24a Shell 6.6–6.8 mm wide, very tightly coiled; no lip teeth; Pacific Coast from Vancouver Island to Oregon ..... *germana*, p. 231

b Shell larger than 8.6 mm, less tightly coiled, lip teeth usually present 25

25a Shell width over 12 mm, lip teeth and parietal lamella small or absent (although lip swelling may be thick) 26

b Shell width below 11.3 mm, lip teeth and parietal lamella medium to large 27

26a Shell width 19–26 mm, lower lip tooth, or the swelling that replaces it, located near columella; west of the Cascade Range, in Washington and Oregon ..... *devia*, p. 230

b Shell width 12–19 mm, lower lip tooth, or the swelling that replaces it, located in middle of lower lip; hybridizes with *m. harfordiana*; east of the Cascade Range, in Oregon, Idaho and Montana ..... *m. mullani*, p. 223

27a Shell width 8.6–10.1 mm, umbilicus very wide; hybridizes with *m. mullani*; restricted to the Snake River valley in Idaho ..... *m. hardfordiana*, p. 227

b Shell width 10.1–11.3 mm, umbilicus narrow and partly covered by reflected edge of peristome; central and northern Idaho ..... *sanburni*, p. 229

28a Embryonic shell with striae and often also with granules; Pacific region; *germana, devia, mullani* or *sanburni*, go back to 24

b Embryonic shell smooth or striated; eastern United States and Canada 29

29a Fossil; shell width 19–25 mm, lip teeth and parietal lamella small; Illinois ..... *f. hubrichti*, p. 212

b Recent 30

30a Sculpture of fine spiral lines with extremely fine transverse lines between them; Mississippi and Missouri valleys, from Iowa to Louisiana ..... *f. fosteri*, p. 210

b Sculpture different 31

31a Lip teeth and parietal lamella small to large 32

b Lip teeth and parietal lamella usually absent, very small if present 33

32a Sculpture of triangular scales, last whorl rounded or bluntly angular at the periphery; hybridizes with *o. obstricta*; from Vermont to Michigan and Tennessee ..... *o. denotata*, p. 206

b Sculpture of short wrinkles, last whorl sharply angular or keeled at the periphery; hybridizes with *o. denotata*; Kentucky and Tennessee ..... *o. obstricta*, p. 205

33a Shell banded, rarely uniformly brown-red or horn colored; from Ohio to Minnesota and Kansas ..... *multilineata*, p. 219

b Shell unicolored 34

34a Shell width 17–20 mm, height 8–12 mm, lip swelling thin; Ozarkian area, from Kansas to Louisiana ..... *divesta*, p. 222

b Shell width 19–42 mm, height 11–31 mm, lip swelling medium to very thick 35

35a Lip swelling very thick, small parietal lamella present, shell often flat; from Quebec to Pennsylvania and North Carolina ..... *dentifera*, p. 218

b Lip swelling moderately thick or very thick, parietal lamella only exceptionally present, shell flat to very high 36

36a Shell with faintly visible grid formed by transverse wrinkles and spiral lines, or smooth and shiny; flatter; intergrades with *a. alboladris* and *a. major*; from Minnesota to Arkansas ..... *a. alleni*, p. 216

b Sculpture of the same elements but much coarser, shell higher 37

37a Shell 20–36 mm wide, less globose; intergrades with *a. alleni* and *a. major*; from Quebec to Michigan and Tennessee ..... *a. alboladris*, p. 213

b Shell 27–42 mm wide, globose; intergrades with *a. alboladris* and *a. alleni*; North Carolina to Alabama ..... *a. major*, p. 214

Subgenus *TRIODOPSIS sensu stricto*

The nominate subgenus is characterized by its small or moderately large, umbilicated shell, and the presence of two lip teeth and a parietal lamella in the aperture. Anatomically, the description of the genus fits the subgenus well. Subgenera *Xolotrema* and *Neohelix* are separated from *Triodopsis* mainly on the basis of shell characters, *Cryptomastix* on the basis of anatomical features and distribution.

The subgenus contains 12 of the 22 species that belong to the genus. Many of the species exhibit great complexity, which makes the classification difficult but provides rich material for evolutionary studies. The species can be grouped in five natural, hence easily recognizable, species complexes. These are: *tridentata, rugosa, juxtidens, fraudulenta,* and *fallax.*

THE *TRIDENTATA* COMPLEX

The *tridentata* complex comprises three closely related forms: *tridentata, complanata* and *burchi.* Of these, *tridentata* and *complanata* are undoubtedly distinct species, while *burchi,* a diminutive form of *complanata,* may be either a distinct species or a subspecies.

The *tridentata* complex shows a close relationship to the *rugosa* complex.

Triodopsis tridentata (Say)
Plate I: 1–8

Helix tridentata Say, 1817, Nicholson's Encyclopedia, 1st American Edition, article "Conchology." "Middle States." Neotype designated by Pilsbry (1940: 790, fig. 474a). Type locality: northern edge of Philadelphia, Montgomery County, Pennsylvania. Neotype and paratypes ANSP 105972.

Triodopsis lunula Rafinesque, 1831, Enumeration and account of some remarkable natural objects in the cabinets of Prof. Rafinesque, in Philadelphia, November 1831: 3. "Kentucky." Types not examined.

Polygyra tridentata edentilabris Pilsbry, 1894, Nautilus, 7: 140. "Cumberland Mountains." Type ANSP 57255.

Definition. The name *tridentata,* as used here, applies to *Triodopsis t. tridentata* and *t. edentilabris* of earlier authors.

Description. Shell width 12.3–20.7 mm; height 5.5–11.0 mm; height to width ratio 0.43–0.57; umbilicus 2.0–4.3 mm; umbilicus to width ratio 0.14–0.24; embryonic whorls 1.4–1.5, with striae and granules below suture, smooth elsewhere; striation more pronounced on subsequent whorls; three wide, low striae per millimeter on last whorl; space between striae always granulated; granules numerous below suture and in umbilical region; aperture oval-triangular; lip swelling marginal; lip teeth moderately developed; lower tooth located at variable distance from juncture of lower lip with shell; parietal lamella slightly angular, pointing at or slightly below upper lip tooth.

Distribution. Triodopsis tridentata occurs in southeastern Canada and eastern and central United States, from Ontario south to Alabama and west to Iowa (Fig. 3). It is entirely absent from the eastern Kentucky-Tennessee area, however, and is there replaced by the related species *Triodopsis c. complanata.* This interesting phenomenon will be discussed in some detail below.

There is, in the ANSP collection, a single specimen of *T. tridentata* (ANSP 57231), collected by A. D. Brown in "Adams County, Missouri." This record appears to be erroneous, since no such county exists in Missouri, and the specimen, judging from its appearance, must have come from farther north.

The *measured material* comes from the following localities. *New Hampshire*: Grafton (2 samples) and Merrimack counties (MCZ). *Vermont*: Orleans, Chittenden, Addison, and Rutland counties (MCZ). *New York*: Albany, Herkimer, Madison, Onondaga, Niagara, Ulster, and Richmond counties (MCZ). *Ontario*: Wellington County (MCZ). *Michigan*: Oakland, Washtenaw, Ingham, and Calhoun (2 samples) counties (MCZ). *Massachusetts*: Hampden and Berkshire counties (MCZ).

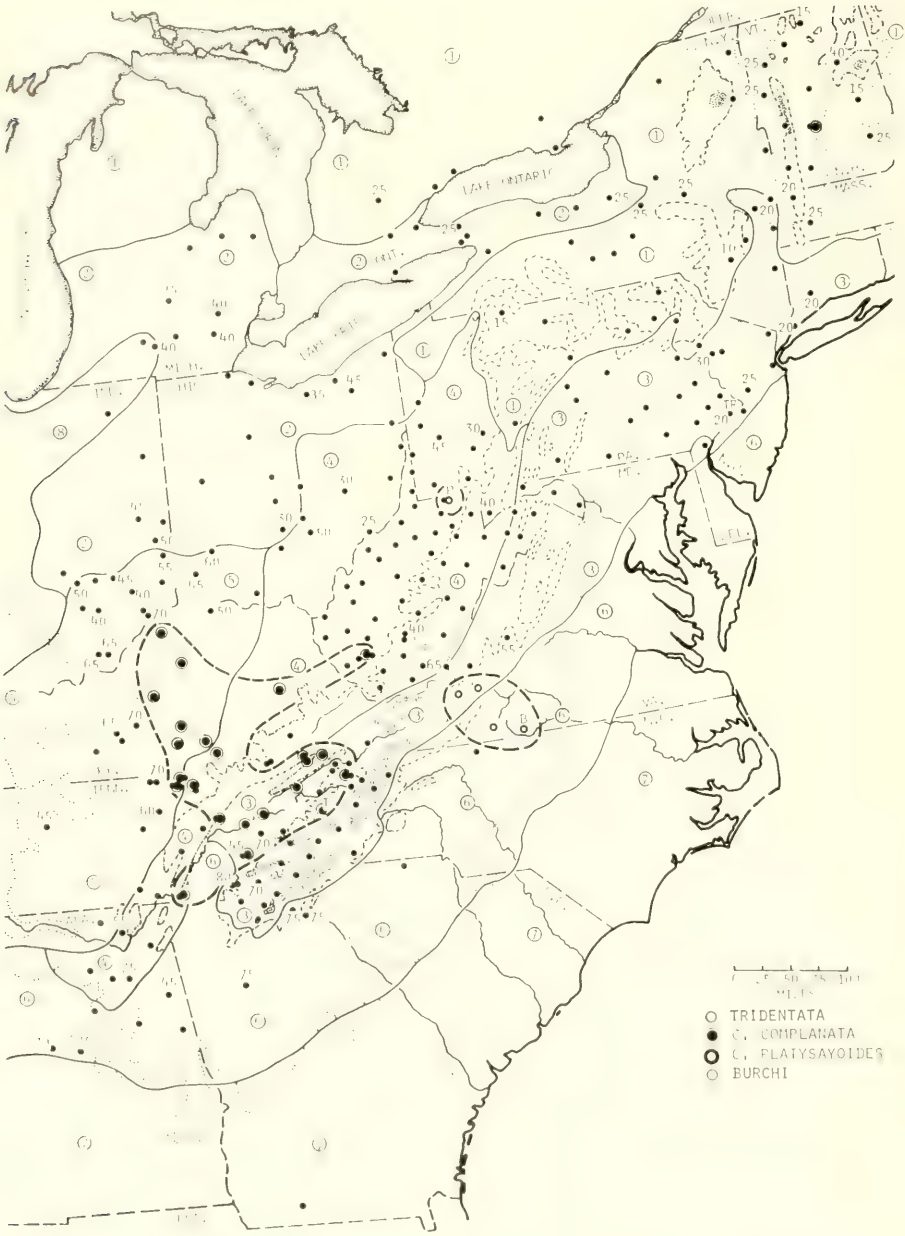


Figure 3. Distribution of *Triodopsis tridentata, complanata,* and *burchi,* and the geographic variation of the character index in *tridentata.* One record of *tridentata* from Illinois and another from Iowa have been omitted. Thick, dashed line surrounds the range of c. *complanata,* c. *platysayoides,* and *burchi.* B, type locality of *burchi;* C, c. *complanta;* P, c. *platysayoides;* T, *tennesseensis,* considered synonymous with c. *complanata;* TR, *tridentata.* Numbers without a circle are mean values of samples in character index; they range from 15 in the north to 80 in the south. Numbers encircled refer to forest types; one, northern hardwood forest; two, beech-maple; three, oak-chestnut; four, mixed mesophytic; five, western mesophytic; six, oak-pine; seven, southeastern evergreen; eight, oak-hickory forest; nine, prairie or grassland; ten, maple-basswood forest (terminology after Braun, 1950). Elevation: . . . . . 500-foot contour line; • — • — • 1500 foot; : : : : : area over 3000 feet. Thin dashed lines mark state boundaries.

Connecticut: Fairfield County (2 samples, MCZ). *New Jersey*: Mercer County (MCZ). *Pennsylvania*: Northampton, Philadelphia, Dauphin, McKean, Indiana, and Allegheny counties (MCZ); Lee County (JV). *Maryland*: Garrett County (MCZ). *West Virginia*: Fayette and Mercer counties (CM). *Ohio*: Summit, Lorain, Washington, Muskingum, Hocking, Pickaway, and Hamilton counties (MCZ). *Indiana*: Fayette, Henry, Franklin, Dearborn, Jennings, Bartholomew, Jackson, Monroe, Harrison, and Crawford counties (MCZ). *Kentucky*: Pendleton, Trimble, Hart, and Edmondson counties (MCZ); Bell County (JV). *North Carolina*: Avery, Yancey, Henderson, Swain, and Cherokee counties (MCZ). *Tennessee*: Sullivan, Sevier, Monroe, Polk, Clay, Cumberland, Putnam, Dickson, and Hamilton counties (MCZ). *Georgia*: Stephens, Habersham, and Fulton counties (MCZ). A total of 80 samples, 1–15 specimens each, 395 specimens altogether.

Ecology. Triodopsis tridentata occurs in northern hardwood, mixed deciduous, and mixed oak-pine forests (Fig. 3, phytogeographic terms after Braun, 1950). In New York and New Jersey it approaches sea level. In the Appalachian Mountains, specifically in the Roan Mountains, Carter County, Tennessee, it ascends to as high as 4000–5000 feet. The latter habitat assumedly still lies in the oak-chestnut forests, which reach up to 4500–5000 feet (Braun, 1950: 206).

Triodopsis tridentata lives in the litter layer of the forests, under fallen logs or other kinds of shelter. Its food is supplied by decaying leaves and the fungi that grow on them. Its ecological niche thus seems to be very similar to that of the related forms *T. c. complanata, j. juxtidens* or *f. fallax*. It is probably because of this similarity that *tridentata* cannot coexist with any of these forms. Should it invade, competition would ensue, which eventually would lead to the exclusion of one or the other (exclusion principle of Hardin, 1960). This may explain the distributional pattern (replacement) of these forms (Figs. 3, 9, 15). The exclusion principle seems also to be at work when *tridentata* overlaps (geographically) other forms of *Triodopsis*, such as *c. platysayoides* or *j. discoidea*. The overlapping forms do not occur together, *tridentata* being confined always to the relatively drier, and the other two the relatively more moist habitats within the zone of overlap. In these cases, then, exclusion led to ecological separation of the (once) competing forms.

Variation. Aperture: Four grades of aperture can be distinguished, based on the shape of the aperture and development of the lip swelling and lip teeth. In grade A the aperture is oval-triangular, the lip swelling moderately and uniformly thick along its entire length and the lip teeth moderately large (Plate I). The aperture of grade B also is oval-triangular, but the lip swelling is somewhat thicker, and the lip teeth larger. In grade C the outer contour of the aperture is oval-triangular. The inner contour of the upper lip runs parallel with the outer contour, but that of the lower lip does not, because the lower lip swelling is higher in the middle than in the corners, thus forming a straight, ledge-like structure; sometimes the upper lip is swollen instead of the lower. The lip swelling generally is thicker than in grade B, and the lip teeth are larger. In grade D the lip swelling is the thickest, the lip tooth the largest, and both the upper and lower lip swellings are straight, like the lower lip swelling of grade C. The four grades form a continuous series, although A-B and C-D are more similar to each other than is B to C.

Similar aperture series occur in *T. fallax*, *T. copei*, *T. mullani*, *T. rugosa*, and *T. fraudulenta*. In all cases except that of *copei* the grades with the heavier armature occupy higher elevations than do those with the lighter armature. This seems to indicate that the heavy armature is an adaptation to

TABLE I

CHART FOR COMPUTING CHARACTER INDEX IN *TRIODOPSIS TRIDENTATA*. METHOD OF CALCULATION: A SPECIMEN WITH A SHELL WIDTH OF 20.5 MM, AN UPPER TOOTH TO LOWER TOOTH RATIO OF 1.10, AND AN APERTURE GRADE D WAS SCORED $(100 + 70 + 30)/2 = 100$, THE AVAILABLE MAXIMUM SCORE.

SCORE	SHELL WIDTH	UPPER TO LOWER TOOTH RATIO	APERTURE GRADE	
0	12.3–12.7	0.69–0.72	A	Northern
5	12.8–13.1	0.73–0.74		populations
10	13.2–13.5	0.75–0.77	B	↑
15	13.6–13.9	0.78–0.80		
20	14.0–14.2	0.81–0.83	C	
25	14.3–14.6	0.84–0.86		
30	14.7–14.9	0.87–0.89	D	
35	15.0–15.3	0.90–0.92		
40	15.4–15.6	0.93–0.95		
45	15.7–16.0	0.96–0.98		
50	16.1–16.3	0.99–1.01		
55	16.4–16.7	1.02–1.04		
60	16.8–17.1	1.05–1.07		
65	17.2–17.5	1.08–1.09		
70	17.6–17.9	1.10–1.13		
75	18.0–18.3			
80	18.4–18.7			
85	18.8–19.1			
90	19.2–19.6			
95	19.7–20.1			↓
100	20.2–20.7			Southern populations

high elevations, but its specific significance is, as yet, unknown (p. 239).

The geographic variation of the aperture is basically clinal, since in the northern parts of the range grade A individuals predominate, in the middle regions grade B, and in the southern, grade C. The grade D specimens, however, do not fit into this pattern, since they occur near the center of the range, instead of in the southern end, as might be expected. This seemingly anomalous distribution makes sense only if we consider that D is a mountain-adapted form, and that the area southeast of the center of the range is mountainous. Thus, it is natural that altitudinal variation is superimposed upon the basically latitudinal, clinal variation.

Measured characters: The shell width (size) is statistically correlated with shell height, umbilicus, and, to a degree, with the ratio of the upper lip tooth distance to the lower lip tooth distance. The species shows an overall size increase in its range from north to south. In the southern half of the range, however, the variation is irregular; we cannot, therefore, speak of a true cline in size.

The height to width ratio and umbilicus to width ratio vary irregularly throughout the entire range. The upper tooth to lower tooth ratio shows a slight and gradual increase from north to south. This ratio is, to an extent, correlated with the aperture grades, grade A specimens having lower, and grade B, C and D specimens increasingly higher ratios. The correlation is not a perfect one, however, because grade B, on the basis of overall similarity, is closer to grade A than to grade C, but according to the upper tooth to lower tooth ratio, it appears to be closer to C than to A.

Character index: The character index was calculated with the aid of the chart shown below (Table I). The mean values of populations in the character index show a gradual increase from north to south (Fig. 3). A relatively sharp character gradient occurs only in the area where the valleys of the Holston and French Broad rivers, and the Yadkin and Catawba rivers cut deeply into the ranges of the Appalachians. These valleys may be responsible for the existence of the gradient, because they probably act as partial barriers to the gene flow along the Appalachian ranges.

The range of variation in the character index is of the same order of magnitude in all measured populations (Fig. 4). Note that in this figure it is not the actually observed ranges which are compared, but the mean expected ranges of hypothetical populations. The observed ranges cannot be directly compared, because they belong to populations of different size, and the range of variation tends to vary with the size of the population. Therefore, we must calculate how large the range of variation would be if the populations were all of the same

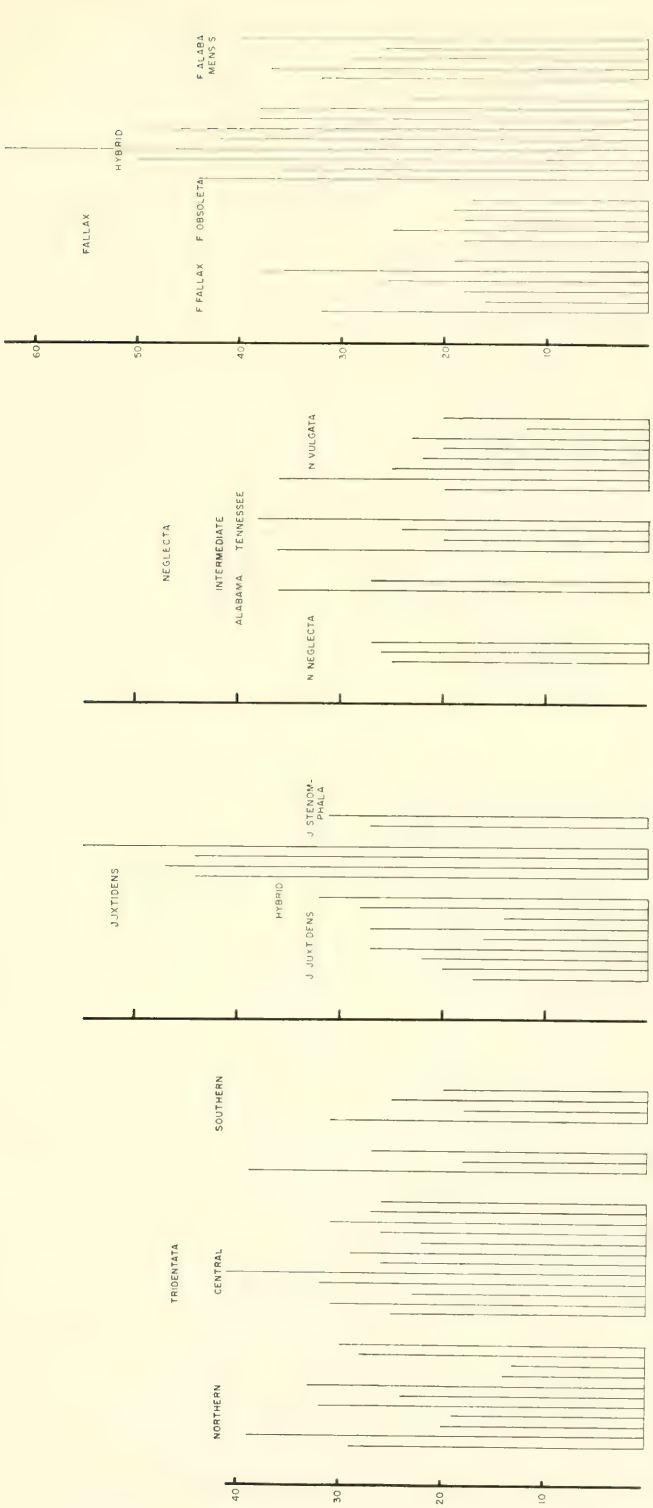


Figure 4. Range of variation in samples of *Triodopsis tridentata, juxtidens, neglecta,* and *fallax*. The range is calculated with the method described on p. 156. Scale in character index units. The range is considerably greater in the hybrid samples than in most other samples. The samples of *f. alabamensis* also have a somewhat wider range than those of *f. fallax* or *f. obsoleta*.

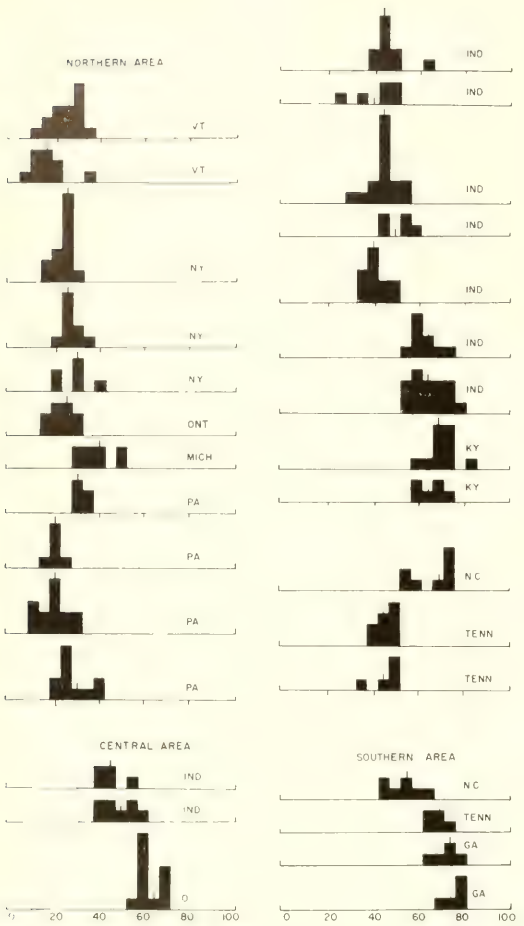


Figure 5. Character index histograms of samples of *Triodopsis tridentata*. Short line on top of column indicates mean value of samples. All histograms are normal or slightly skewed. The abbreviations stand for the states where the samples have been collected. Scale in character index units.

size. This can be done by using Simpson's method (1941), which, briefly, consists of multiplying the standard deviation of the actual populations by an appropriate factor, e.g., 6.48 if N = 30 is selected as the standard population size. The hypothetical ranges thus obtained can be directly compared. These ranges for all *tridentata* populations are of the same order of magnitude, which indicates that the variation of the species is primary. (Should secondary intergradation be the case, the intergrading populations would be expected to show greater variation than the others.) This conclusion is supported by the fact that the distribution curves of the populations in the character index are normal (Fig. 5), whereas those of hybrid populations are skewed (see histograms of *T. juxtidens* and *T. fallax*, Figs. 11 and 18).

Systematics. *Triodopsis tridentata* of Pilsbry (1940) and most contemporary authors is an oversized, artificial taxon. It is said to consist of six subspecies, but, in my opinion, four of these should be excluded and the other two should be combined. Those to be excluded are *T. t. complanata, t. tennesseensis, t. juxtidens,* and *t. discoidea*; those to be combined are *t. tridentata* and *t. edentilabris*. *Triodopsis t. edentilabris* (Pl. I, figs. 5, 6) of the "Cumberland Mountains" differs from *tridentata* in lacking the lip teeth, although the lip swelling is normally developed, and in having more obese whorls and a shorter and higher aperture. It must be admitted that these specimens are "recognizably different" from *tridentata*. But toothless specimens, which approach *edentilabris*, occur in many populations of *tridentata*. Also, it must be kept in mind that there are only three known specimens of *edentilabris*; thus, we cannot expect to find much intergradation. For these reasons, I prefer to consider *edentilabris* a synonym of *tridentata*. The distributional data allow this conclusion, since *edentilabris* is only known from a single locality somewhere in the Cumberland Mountains, which lie within the range of *tridentata*.

The difference between the northern and southern populations of *tridentata* is as great as that between different species. It may therefore seem desirable to separate these populations on the subspecies level. Because, however, the two populations intergrade without a convenient break which would allow a natural division between them, it seems better to keep them in a single taxon.

Evolutionary relationships. *Triodopsis*

tridentata is probably the stock from which developed the related species *T. complanata* and *T. burchi*. It has a three-toothed aperture and a striated shell, whereas *complanata* and *burchi* have reduced dentition and smooth or striated shells. The *tridentata* features can be considered primitive, because they are common in many unspecialized species of *Triodopsis*. The features of *complanata* and *burchi* are presumably more advanced, because they occur in a few species which may well be ecologically specialized.

Summary. (1) *Triodopsis tridentata* is a monotypic species. It corresponds to the former *T. tridentata tridentata*, to which the former *t. edentilabris* is added as a synonym.

(2) *Triodopsis tridentata* is distributed in eastern North America from Ontario south to Alabama and west to Iowa. In eastern Kentucky and eastern Tennessee it is replaced by the related form *T. c. complanata*.

(3) *Triodopsis tridentata* lives in the litter layer of mixed deciduous and oak-pine forests, ranging from low to high elevations. It shows habitat exclusion with *T. c. complanata*, *j. juxtidens*, and *f. fallax*, and with *T. c. platysayoides* and *j. discoidea*.

(4) The geographic variation of certain features is clinal, that of others irregular. There is a continuous intergradation between the extreme northern and the extreme southern populations in combined character index. The range of variation is essentially the same in all populations.

(5) *Triodopsis tridentata* is probably ancestral to *T. complanata* and *T. burchi*.

Triodopsis complanata (Pilsbry)
Triodopsis complanata complanata (Pilsbry)

Plate I: 9–11

Polygyra tridentata var. *complanata* Pilsbry, 1898, Nautilus 12: 22. Burnside, Pulaski County, Kentucky. Type ANSP 71399.

Polygyra tridentata var. *tennesseensis* Walker and Pilsbry, 1902, Proc. Acad. Nat. Sci. Philadelphia 54: 422. Foot of the high bluffs on south side of French Broad River below Paint Rock, Madison County, North Carolina. Type ANSP 84022.

Definition. *Triodopsis c. complanata* combines the former *T. tridentata complanata* and *t. tennesseensis*.

Description. Shell width 16.7–23.3 mm; height 8.0–10.6 mm, height to width ratio 0.40–0.54; umbilicus 2.9–6.0 mm, umbilicus to width ratio 0.17–0.26; embryonic whorls 1.4–1.5, with dense striae and long, transverse granules; two subsequent whorls almost exclusively with granules, then striation becoming more pronounced, 3–4 low to moderately high striae per millimeter on last whorl; intervals between striae with granules; incised spiral lines appearing after breakage; aperture oval-triangular; lip swelling well developed, marginal or sometimes bulging in vicinity of upper lip tooth; lip teeth very small, sometimes only bare traces, rarely moderately large; upper lip tooth rather close to juncture of upper lip with shell; distance between lip teeth nearly as great as distance of upper lip tooth from juncture of upper lip with shell; parietal lamella short, pointing well below upper lip tooth.

Differential diagnosis. *Triodopsis c. complanata* is best distinguished from *T. tridentata* on the basis of apertural features. The lip swelling is very close to the edge of the aperture, so that the latter appears swollen, especially in the vicinity of the upper lip tooth. The lip teeth are small, sometimes barely discernible, rarely moderately large; the distance between the upper and lower lip teeth is nearly as great as the distance between the upper lip tooth and the juncture of the upper lip with the shell (Fig. 6). The parietal lamella is short and straight, corresponding to the distal portion of the parietal lamella of *tridentata*, and when looking at the shell from below, points well below the upper lip tooth. In *tridentata*, the lip swelling is moved back slightly from the peristome, so that the latter is relatively sharp. The lip teeth are medium to well developed; the distance

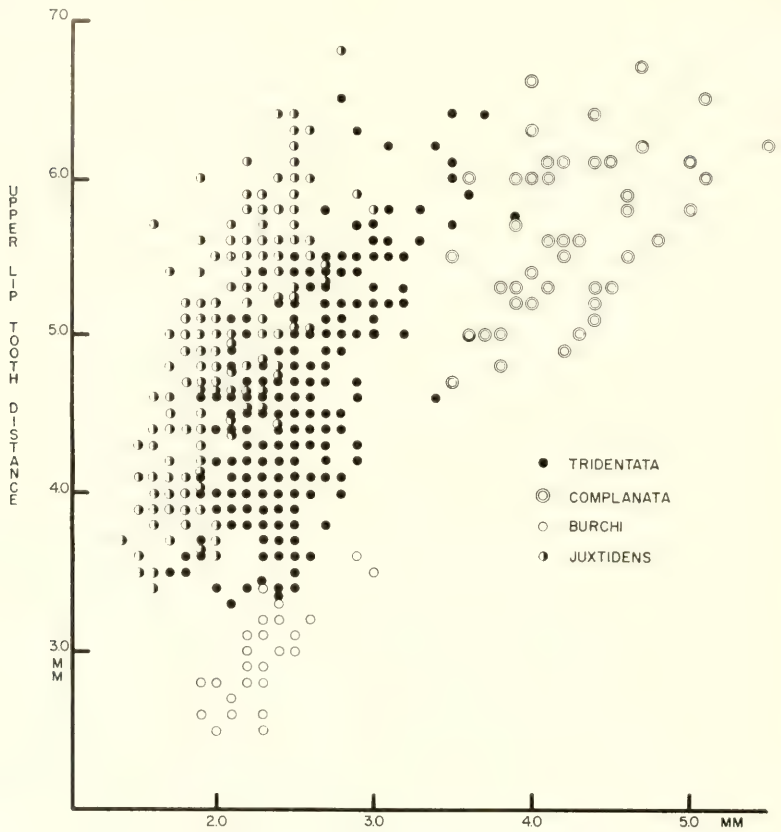


Figure 6. Scatter diagram of upper lip tooth distance (ordinate) versus distance between upper and lower lip teeth (abscissa) in *Triodopsis tridentata, complanata, burchi,* and *juxtidens.* Each dot represents one or more specimens. Scale in millimeters.

between the upper and lower lip teeth is definitely smaller than the distance between the upper lip tooth and the juncture of the upper lip with the shell. The parietal lamella is long and slightly angular; it points to or slightly below the upper lip tooth. Further differences are in the shell. *Triodopsis c. complanata* is larger and flatter than *tridentata,* although there is a wide overlap. Also, *c. complanata* is sometimes smooth and glossy, whereas *tridentata* is always striated. Striated *c. complanata* shells with relatively well-developed teeth may be difficult to separate from *tridentata.*

Pilsbry emphasizes the similarities between *c. complanata* and *j. discoidea,* saying that, "Except in the widely separated and weaker lip teeth it [*c. complanata*] resembles *T. t. discoidea* . . . ." (1940: 801). I believe that Pilsbry was describing only a superficial similarity caused by the glossiness of the shell. *Triodopsis t. discoidea* (*j. discoidea*) in reality belongs to quite another species complex, *juxtidens.*

Distribution. Triodopsis c. complanata occurs in Kentucky, Tennessee, and the adjoining regions of West Virginia, Virginia, and North Carolina (Fig. 3). It is remarkable that the related species, *T. tridentata,* which occurs from Ontario south to Alabama, is largely absent from this

area. This replacement will be discussed in the section on ecology.

In the MCZ collection there is a specimen allegedly from Mt. Ascutney, Windsor County, Vermont (MCZ 49268, from the Stearns Collection). This locality is so far outside the normal range that its correctness is questionable.

The *measured material* comes from the following localities (Fig. 3). *West Virginia*: Logan County (2 samples, JV). *Virginia*: Scott County (MCZ). *Kentucky*: Henry, Marion, Casey, Pulaski, and Russell counties (MCZ); Pulaski (2 samples), Breathitt and McCreary counties (ANSP). *Tennessee*: Washington, Monroe, Hancock, and Overton counties (MCZ); Hamblen, Knox, Morgan, and Hamilton counties (ANSP). *North Carolina*: Madison County (ANSP). A total of 22 samples, 1–11 specimens each, 65 specimens altogether.

Ecology. Triodopsis c. complanata occurs in oak-chestnut, mixed mesophytic, and western mesophytic forests, between 500 and 1500 feet elevation (Fig. 3). The forest boundaries do not coincide with the subspecies borders. Nor do the contour lines, except in the eastern part of the range, where the subspecies border closely follows the 1500 foot line.

Triodopsis c. complanata is absent from the territory of *T. tridentata* nearly everywhere (Fig. 3). The apparent reason is that the two species, which are of similar size and also of similar living habits, compete with each other; given enough time, one will exclude the other. This phenomenon of exclusion (Hardin, 1960) provides an explanation of the geographical replacement of *tridentata* with *c. complanata*, mentioned above.

Variation. The sculpture is correlated with the habitat to the extent that smooth and shiny shells only occur in places near water, whereas striated shells occur both near and far away from water. It is possible that the smooth sculpture is caused by the high degree of humidity of the habitat (Rensch, 1932), but there are no experimental data available.

The measured characters are statistically correlated with each other; their geographic variation is irregular.

Systematics. Triodopsis c. complanata as defined in this paper combines the former *T. tridentata complanata* and *t. tennesseensis*. The combination of these forms is justified on morphological and distributional grounds. The former is said to have a smooth shell, the latter a striated one. In fact, however, many specimens occur with finely striated shells which may belong to either of the two "subspecies." The two forms do not have separate ranges either; instead, the striated form surrounds and "overlaps" the smooth form, which occurs in a very restricted area. Thus, to consider the smooth population a subspecies would amount to calling an ill-defined and localized form a subspecies, which, I believe, should be avoided. The irony of the situation is that the name of the more widely distributed form, *tennesseensis*, is newer than that of the restricted form, *complanata*, and therefore the former must be considered a synonym, and the latter the valid name.

Triodopsis c. complanata must be specifically separated from *T. tridentata*. It overlaps and in a few places coexists with *tridentata* without interbreeding, which proves that it is specifically distinct from that species.

Triodopsis complanata platysayoides (S. T. Brooks)

Polygyra platysayoides Brooks, 1933, Nautilus 46: 54. Cooper's Rock, Monongalia County, West Virginia. Type not seen.

Definition. Triodopsis c. platysayoides is the former *T. platysayoides*.

Description and differential diagnosis. Triodopsis c. platysayoides differs from *c. complanata* in the larger dimensions of the shell and the more cylindrical umbilicus. The width of the shell is 26.5 mm (16.7–23.5 mm in *c. complanata*); height 10.5

mm, height to width ratio 0.40; umbilicus 60 mm, umbilicus to width ratio 0.23 on the only specimen which was fit for taking measurements. The shell is finely striated and shiny. The lip teeth are absent, but the lip swelling is somewhat thicker in those places where the lip teeth would occur. The umbilicus is almost as wide at the beginning as at the later whorls; thus it is more cylindrical than the umbilicus of *c. complanata.*

Distribution. Triodopsis c. platysayoides is a geographical isolate of *c. complanata.* It is known only from a single locality in northern West Virginia, Cooper's Rock State Park in Monongalia County, about 150 miles away from the area of *c. complanata* (Fig. 3). Two samples, 4 specimens altogether, have been studied.

Ecology. The habitat in which *T. c. platysayoides* lives is a deep canyon of the Cheat River, between 1000 and 1300 feet elevation. We failed to find the snail on the hills which surround the canyon. Only *T. tridentata* was found on these hills. This arrangement seems very similar to that found between *T. c. complanata* and *T. tridentata,* and thus it seems likely that ecological exclusion is also involved here.

Variation. Because of the extremely small population, there is no variation to speak of.

Systematics. Triodopsis c. platysayoides is usually ranked as a full species in the contemporary literature. It is more likely, however, that it is conspecific with *T. c. complanata,* because they are morphologically remarkably similar. The similarity is so great, indeed, that, should populations be found in the area that presently isolates them, intergradation could be expected to occur. It stands to reason, however, that *platysayoides* should have subspecific rank, because it is geographically isolated from the main population of *complanata.*

Summary. (1) *Triodopsis complanata* consists of two subspecies: *c. complanata* and *c. platysayoides.* The nominate subspecies combines the former *T. tridentata complanata* and *t. tennesseensis,* whereas *c. platysayoides* corresponds to the former *T. platysayoides.*

(2) The two subspecies of *T. complanata* are geographically isolated from each other. The nominate subspecies geographically replaces *T. tridentata.*

(3) Both subspecies favor low areas. Here they can compete successfully with the related species, *T. tridentata,* which is more successful at higher elevations. The two species as a rule do not invade each other's habitat, thus showing ecological exclusion.

(4) The sculpture seems to vary with the wetness of the habitat to some extent. Other characters show irregular geographic variation.

Triodopsis burchi Hubricht
Plate I: 12–14

Triodopsis tennesseensis subsp. *burchi* Hubricht, 1950, Nautilus 64: 8. From along Route U.S. 58, 3 miles west of Danville, Pittsylvania County, Virginia. Type ANSP 186178.

Definition. Triodopsis burchi corresponds to the former *T. tennesseensis burchi* (*T. tennesseensis* is considered a synonym of *T. c. complanata*).

Description. Shell width 8.9–13.2 mm; height 4.9–6.2 mm, height to width ratio 0.45–0.56; umbilicus 1.5–2.7 mm, umbilicus to width ratio 0.15–0.21; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; subsequent whorls with more pronounced striae, last whorl with 3–4 striae per millimeter; intervals between striae smooth or with granules; umbilical region and shoulder of last whorl always with granules; in some specimens, fine spiral lines (20 per mm) also present near aperture; lines worn off easily, leaving smooth shell; aperture oval-triangular, upper side gently curving, lower almost straight; lip swelling thick to very thick, upper lip swelling bulging near lip tooth; lip teeth moderate to small to almost none; upper to lower tooth ratio 0.78–0.92; parietal lamella moderate to small, corresponding to distal

portion of a full parietal lamella, pointing well below upper lip tooth.

Differential diagnosis. *Triodopsis burchi* "differs from *T. tennesseensis* [*T. c. complanata*] in being much smaller, with a more glossy surface" (Hubricht, 1950b). The two forms are otherwise nearly identical. The glossiness of the shell is due to the almost complete lack of granules on the last whorl; in *c. complanata* this is granulated and hence dull.

Distribution and ecology. *Triodopsis burchi* is a geographical isolate of *T. c. complanata* (Fig. 3). The Blue Ridge and the Appalachian mountains isolate the two forms. There is a distance of about one hundred miles between the closest *burchi* and *c. complanata* localities. The range of *burchi* is confined to the Inner Piedmont of Virginia, from Pittsylvania County to the Blue Ridge Mountains. The area is covered by mixed oak-pine and oak-chestnut forests. The elevation ranges from 500 to 1500 feet.

The *measured material* comes from the following localities: *Virginia*: Pittsylvania, Henry, and Roanoke counties (ANSP). A total of 3 samples, 2–15 specimens each, 29 specimens altogether.

Variation. As can be expected because of its small population and restricted distribution, the variation of *T. burchi* is limited.

Systematics. *Triodopsis burchi* was originally ranked by Hubricht as a subspecies of *T. tennesseensis* [*T. c. complanata*]. More recently (1958), he ranked the taxon as a full species, without stating his reasons for the change. It seems to me that either arrangement is acceptable. The only thing that could settle the question, i.e., whether or not the two forms are reproductively isolated, is not known, since they are not in contact in nature. If we assume, as is done here, that the great difference in body size between *burchi* and *c. complanata* could prevent interbreeding, we may assign *burchi* full specific rank. Otherwise we may consider it a subspecies of *T. complanata*.

Summary. *Triodopsis burchi* is a geographic isolate of *T. c. complanata*, and is presumably reproductively isolated from that species. It is distributed over a small and uniform area. Its variation is limited.

Evolutionary relationships in the complanata-burchi group. *Triodopsis c. platysayoides* and *T. burchi* are peripheral isolates of *T. c. complanata*, which is an indication that they are relatively recent descendants of the latter form. The fact that *burchi* is much smaller and *c. platysayoides* is larger than *c. complanata* is consistent with this interpretation, since peripheral isolates are the most variable elements of a population (Mayr, 1963). Still another fact supporting the above interpretation is that *c. complanata* has either a smooth or a coarsely striated shell, whereas the two other forms have smooth or finely striated shells. A coarsely striated shell is generally a primitive feature in *Triodopsis* (p. 157).

The *complanata-burchi* group probably evolved from *tridentata*.

THE *RUGOSA* COMPLEX

Definition. The *rugosa* complex contains two taxa, *rugosa* and *fulciden*, which can be considered either distinct species or conspecific subspecies.

Triodopsis rugosa Brooks and MacMillan Plate I: 15–18

Triodopsis tridentata var. *rugosa* Brooks and MacMillan, 1940, Nautilus 53: 96, pl. 12, fig. 3. Damp ravine, Blair Mountain, 1 mile southwest of Blair, Logan County, West Virginia. Paratype ANSP 174909.

Triodopsis rugosa var. *anteridon* Pilsbry, August 1, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 803, fig. 477. Valley Forge, Carter County, Tennessee. Type ANSP 150304.

Definition. *Triodopsis rugosa* combines the former *T. r. rugosa* and *r. anteridon*.

Description. Shell width 10.6–15.5 mm; height 5.4–7.2 mm, height to width ratio 0.42–0.54; umbilicus 1.7–3.6 mm, umbilicus to width ratio 0.16–0.23; embryonic whorls

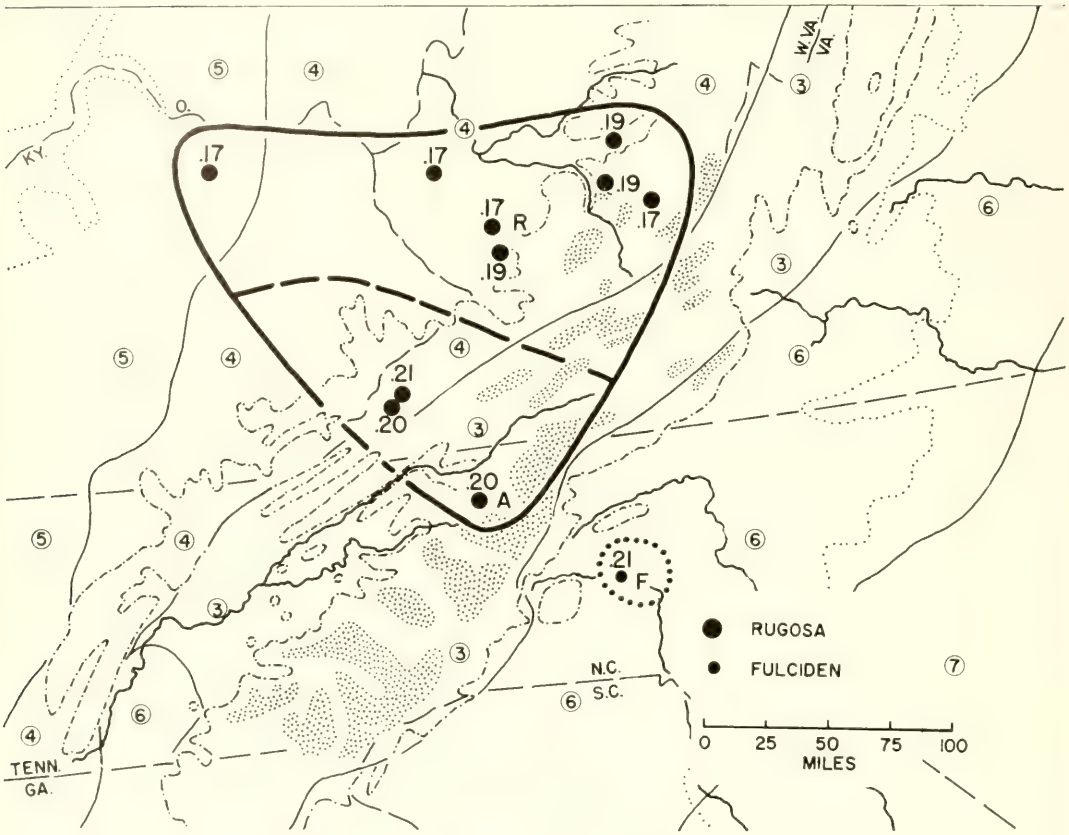


Figure 7. Distribution of *Triodopsis rugosa* and *fulciden*, and the geographic variation of the umbilicus to width ratio in *rugosa*. Thick, solid line surrounds the range of *rugosa*; thick, dashed line separates the samples with a narrow umbilicus (umbilicus to width ratio 0.17–0.19) from those with a somewhat wider umbilicus (0.20–0.21); dotted line surrounds the range of *fulciden*. A, type locality of *anteridon*, considered synonymous with *rugosa*; F, *fulciden*; R, *rugosa*. Numbers without a circle are mean values of samples in umbilicus to width ratio. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

1.4–1.5, with striae below suture; striation becoming more pronounced on subsequent whorls; last whorl with 4–5 striae per millimeter; intervals of striae with fine, oblong granules or delicate spiral lines except on shoulder, which is always granulated; aperture trapezoid, or upper side rounded, lower straight; upper lip swelling thin to very thick, lower lip swelling always thick, forming a straight ledge; upper lip tooth often smaller than lower, somewhat receding, and supported below by a slanting buttress; lower tooth located at or to the left of middle of lower lip; parietal lamella straight, bladelike and outstanding, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis rugosa* differs from the members of the *tridentata* complex in that the shape of the aperture is a trapezoid (sometimes with a rounded upper side); the upper lip tooth is receding, often smaller than the lower lip tooth, and has a slanted buttress below; the parietal lamella is large and points above the upper lip tooth. In the *tridentata* group, the aperture is oval-triangular, the upper lip tooth is not receding or buttressed, the two lip teeth are equally developed, the parietal

lamella is of normal size and points below the upper lip tooth.

Triodopsis rugosa differs from *T. pendula* in that the upper lip tooth is often smaller than the lower lip tooth and is buttressed; the lower lip tooth is near the middle of the lip; the last whorl behind the aperture is less than 1½ times as wide as the penultimate, whereas in *pendula* the upper lip tooth is of normal size or even broader than normal, and not buttressed; the lower lip tooth is to the left of the middle of the lip, and the last whorl behind the aperture is 1½ to 2 times as wide as the penultimate one.

Distribution. Triodopsis rugosa is found in a small area which joins West Virginia, Virginia, Kentucky and Tennessee. The *measured material* comes from the following localities (Fig. 7): *Virginia*: Wise County (ANSP, 2 samples; MCZ, 1 sample). *West Virginia*: Greenbrier, Nicholas, Fayette, Lincoln, and Logan counties (CM); Logan County (ANSP, 1 sample; JV, 1 sample). *Kentucky*: Fleming County (ANSP). *Tennessee*: Carter County (ANSP, 1 sample; JV, 1 sample). A total of 13 samples, 1–8 specimens each, 44 specimens altogether.

Ecology. Triodopsis rugosa occurs in oak-chestnut, mixed mesophytic, and western mesophytic forests (Fig. 7). Most localities are in low mountains, around 1500 feet elevation. Brooks and MacMillan stated (1940) that *rugosa* "is found particularly in ravines and valleys that are narrow and damp." The mountainous character of the range is reflected in the variation of the aperture, as discussed below.

Variation. Aperture: The lip swelling and the parietal lamella vary from thin to very thick. From the observation that several species of *Triodopsis* (*tridentata, fraudulenta, f. fallax, m. mullani*) have a stronger armature at high elevations than at low ones, one can infer that this is the case also in *rugosa*. I do not, however, have information on the exact elevation at which the samples were collected; thus this has not been confirmed. The significance of the strong armature is not known.

Sculpture: The intervals of the striae on the last whorl are covered by papillae, fine spiral lines or, in places, by structures intermediate between papillae and spiral lines. The latter structures can be envisioned as papillae with linear extensions on the two sides. Through these structures, the papillae and spiral lines intergrade. Shells with predominantly papillose sculpture occur in the northern and western parts of the range, those with spiral lines, in the southern and eastern parts (Fig. 8).

Measured characters: The width of the shell is correlated with height and umbilicus, not with aperture or sculpture. All characters show irregular geographic variation, except the umbilicus to width ratio, which increases from north to south (Fig. 7). The discordancy between the variation of the latter character and shell width is evident. Therefore, these characters should not be used as the basis for dividing the species into subspecies. Unfortunately, exactly this was done by Pilsbry (1940).

Systematics. According to Pilsbry (1940), *Triodopsis r. anteridon* (Pl. I, figs. 17, 18) is larger, more finely striated, and has a larger umbilicus than *T. r. rugosa*. It may be added that *anteridon* also has a weak armature and a sculpture of spiral lines, whereas *rugosa* has a strong armature and strong papillae. The distinction breaks down, however, when populations other than the type population are considered. Thus, populations from Lincoln and Logan counties, West Virginia, have strong armature and papillae like *rugosa*, but are as large as *anteridon*; their umbilicus is intermediate between the two. Conversely, another population from Fayette County, West Virginia, has the spiral lines of *anteridon*, the small size of *rugosa*, and an intermediate umbilicus and aperture. The conclusion is that *anteridon* cannot be taxonomically separated from *rugosa*. It is, rather, a synonym of the latter.

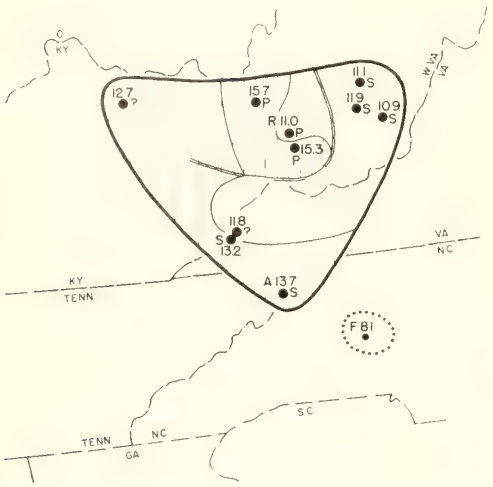


Figure 8. Geographic variation of size (shell width) and sculpture in *Triodopsis rugosa* and *fulciden*. S, spiral sculpture; P, papillate sculpture; ?, sculpture not examined; thin, parallel line separates the samples with papillate sculpture from those with spiral sculpture. Numbers are mean values of samples in size, expressed in millimeters; samples with small size, 10.9–11.0 mm, are separated from the intermediate ones, 12.7–13.7 mm, and the large ones, 15.3–15.7 mm, by a single, thin, solid line. The variation of the two characters is discordant. For other symbols, see Figures 3 and 7.

Summary. *Triodopsis rugosa* is a monotypic species; it includes *T. r. anteridon* as a synonym. It occurs in a relatively small and mountainous area. The aperture probably varies according to the elevation of the habitat; the umbilicus to width ratio varies clinally from north to south; other characters vary irregularly. The variation is thus discordant.

Triodopsis fulciden Hubricht
Plate I: 19–21

Triodopsis fulciden (*sic!*) Hubricht, 1952, Nautilus 65: 81. Upland oak woods, 3.4 miles west of Conover, Catawba County, North Carolina. Holotype ANSP 188292, paratypes ANSP 188290.

Definition. The name *fulciden* is used here as proposed by its author.

Description. Shell width 7.7–8.6 mm; height 4.0–4.3 mm, height to width ratio 0.49–0.53; umbilicus 1.4–1.9 mm, umbilicus to width ratio 0.18–0.23; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striation becoming more pronounced on subsequent whorls; 3–4 striae per millimeter on last whorl; no fine sculpture visible on the studied shells, which were slightly worn; aperture a trapezoid with rounded upper arch; upper and lower lip swelling thick, forming an angle in right lower corner of aperture; upper lip tooth small, having a slanted buttress below, lower lip tooth of normal size; parietal lamella large, straight, outstanding, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis fulciden* differs from *T. rugosa* in its smaller size; otherwise they are very similar. They are comparable to *T. burchi* and *T. complanata* in this respect; these are also extremely similar except for body size.

Hubricht states that "*T. rugosa* . . . has an aperture very similar to *T. tridentata*, whereas the aperture of *T. fulciden* is more suggestive of *T. fraudulenta*" (1952a: 81). To me, the aperture of *fulciden* is not at all similar to that of *fraudulenta*.

Distribution and ecology. *Triodopsis fulciden* is confined to the Catawba River Valley, in Catawba County, North Carolina (Fig. 7). This area lies in the Piedmont region of the Appalachians, between 1000 and 1500 feet elevation. It is covered by mixed oak-pine forests. Only 3 samples, 9 specimens altogether, were available for study from the ANSP and my own collecting.

Triodopsis fulciden is a geographical isolate of the related species *T. rugosa*, which lives west of the Appalachians (Fig. 7). The horizontal distance is only about 65 miles between the two species, but this is enough to isolate them well, since the high ranges of the Appalachians stretch across this area. This distribution shows a conspicuous resemblance to that of *T. complanata* and *T. burchi*, which probably results from similar evolutionary history.

Variation. This is limited, as can be ex-

pected from the small population and the restricted range of the species.

Systematics. Triodopsis fulciden is treated here as a taxon specifically separate from *T. rugosa*, on the assumption that the two forms are reproductively isolated because they differ pronouncedly in body size. It is admitted, however, that this assumption cannot be tested, since the two forms are allopatric in distribution. Such cases are manifestations of what Wilson and Brown (1953) call the "uncertainty principle" in taxonomy.

Evolutionary relationships. Triodopsis fulciden is a peripheral isolate of *T. rugosa*, and on this basis it seems certain that it evolved from the latter in relatively recent times, through geographical isolation. The *rugosa* complex is closely related to the *tridentata* complex. It is not known, however, when the two groups became separated.

Summary. Triodopsis fulciden is a geographic isolate of *T. rugosa*. It has probably achieved reproductive isolation from that form. It occupies a small area; its variation is limited.

THE *JUXTIDENS* COMPLEX

Definition. This complex contains a single species, *T. juxtidens*, with three subspecies: *j. juxtidens*, *j. stenomphala*, and *j. discoidea*. There is some question, however, as to whether the last subspecies should properly be included in *T. juxtidens*, or should be considered a separate species.

Triodopsis juxtidens (Pilsbry)
Triodopsis juxtidens juxtidens (Pilsbry)
Plate II: 1–3

Polygyra tridentata var. *juxtidens* Pilsbry, 1894, Proc. Acad. Nat. Sci. Philadelphia 46: 20, pl. 1, fig. 8. Limestone region, Cave Town, Washington County, Maryland. Type ANSP 64720.

Polygyra tridentata juxtigens F. C. Baker, 1898, Trans. St. Louis Acad. Sci. 8: 84. Pinnacle Hill, southeast Rochester, Monroe County, New York.

Definition. Triodopsis j. juxtidens corresponds to a portion of the former *T. tridentata juxtidens*. The other portion is *T. j. stenomphala*, described in the present paper as a new subspecies (p. 169). *Triodopsis j. juxtidens* contains those populations of the species which have mean values of 60–90, occasionally 55, in character index. The method of computing character index is shown in Table II.

Description. Shell width 11.0–19.1 mm; height 5.3–9.9 mm, height to width ratio 0.46–0.61; umbilicus 1.7–3.5 mm, umbilicus to width ratio 0.12–0.19; number of whorls 4.7–6.0, whorl to width ratio 0.29–0.46; embryonic whorls 1.4–1.5, finely striated below suture, smooth elsewhere; subsequent whorls with regular and more pronounced striation, 3.4 striae per millimeter on last whorl; intervals between striae with sparse granulation, except in umbilical region where granulation is dense; aperture square to circular; lip swelling and lip tooth nearly marginal to slightly receding; when circular aperture combines with receding lip swelling and lip teeth, aperture is called dish-like; upper lip tooth is slightly receding, usually broadened, sometimes bifid; lower lip tooth marginal; upper and lower lip teeth in close proximity (hence the name "*juxtidens*"); parietal lamella arcuate to straight, pointing above upper lip tooth, its proximal portion often low, like a callus.

Differential diagnosis. Triodopsis j. juxtidens differs from *T. tridentata* in that the upper and lower lip teeth are close together, and therefore the distance between them is smaller than the distance between the upper lip tooth and the juncture of the upper lip with the shell (Fig. 6); also, the upper lip tooth is usually broadened and slightly receding, with the parietal lamella pointing above it. In *T. tridentata* the lip teeth are farther apart, the upper lip tooth is very rarely broadened or receding, and the parietal lamella points at or below the upper lip tooth. *Triodopsis n. vulgata*, another similar form, has a wider umbilicus and a more capacious last whorl than *T. j. juxtidens*, and an upper lip tooth that is much broader and deeply receding.

Distribution. Triodopsis j. juxtidens

Table II

Chart for Computing Character Index in *Triodopsis juxtidens*. Method of Calculation: a Specimen Having a Width of 18.0 mm, an Umbilicus to Width Ratio of 0.18, a Whorl to Width Ratio of 0.30, a Parietal Lamella to Width Ratio of 0.17, and an Aperture of "*juxtidens*" Was Scored 30 + 15 + 15 + 20 + 20 = 100, the Available Maximum Score.

Score	Width in mm	Umbilicus to width ratio	Whorl to width ratio	Parietal lamella to width ratio	Aperture	
0	9.8–10.9	0.9–0.10	0.46–0.51	0.30–0.32	*stenomphala*	*j. stenomphala*
5	11.0–12.1	0.11–0.13	0.40–0.45	0.26–0.29		
10	12.2–13.3	0.14–0.16	0.34–0.39	0.22–0.25	intermediate	
15	13.4–14.6	0.17–0.19	0.29–0.33	0.18–0.21		
20	14.7–15.9			0.15–0.17	*juxtidens*	
25	16.0–17.1					
30	17.2–18.3					*j. juxtidens*

ranges along the eastern seaboard from Vermont to Georgia and westward to West Virginia (Fig. 9). It slightly overlaps *T. tridentata*, as discussed below.

A record from Davenport, Scott County, Iowa (MCZ 47473, ex J. D. King) appears to be incorrect, since this locality lies very far outside the normal range. I also regard the records from Isle au Haut, Knox County, Maine (MCZ 14685, 14686 and 14687) as suspect, because the record is outside the normal range, and the habitats on the island (coniferous forests) seem unsuitable for the snail. Three days were spent in an attempt to verify this record, but without success.

The occurrence of *T. j. juxtidens* in West Virginia was first reported by MacMillan (1950). Since Pilsbry in his comprehensive work (1940: 799) explicitly stated that "It [*j. juxtidens*] is not known to occur west of the mountains," verification of the West Virginia records seemed desirable. Half of MacMillan's *j. juxtidens* material indeed proved to be misidentified *T. tridentata* or *T. rugosa*, but the other half was "good" *j. juxtidens*. The occurrence of the subspecies on the western side of the Appalachians thus can no longer be doubted.

This extension of the range of *j. juxtidens* to the western side of the Appalachians probably took place in recent times. We can infer this from two facts. First, only a single valley system has been colonized. The MacMillan collection covers all of West Virginia, and contains enough material to state this with confidence. Secondly, the colonizing population as a whole has not yet become morphologically different (except for one single deme that is intermediate between *j. juxtidens* and the western subspecies, *j. discoidea* [p. 173]). If this inference is true, the snail must have moved at least 90 miles down the valley in a few thousand years, a relatively "fast" dispersal rate for the slow-moving snails. It is probable that this was accomplished, in part at least, by rafting or being washed down the Kanawha River. Similar inferences can be drawn from the distribution of *T. fraudulenta* and *T. m. mullani*.

At present the colonizing populations have approached to within 110 miles of the eastern range limits of *j. discoidea*, the most westerly occurring subspecies. It will be interesting to observe what happens when the two forms establish actual contact.

T. j. juxtidens crossed the mountains through the upper valleys of the Kanawha and Roanoke river systems (Fig. 9). The effectiveness of valleys as dispersal routes is emphasized by the fact that several other cases are known in *Triodopsis* in which the snails have used similar paths of dispersal. Thus a stock of *T. c. complanata* reached the eastern side of the Appalachian Mountains via the Holston and Roanoke val-

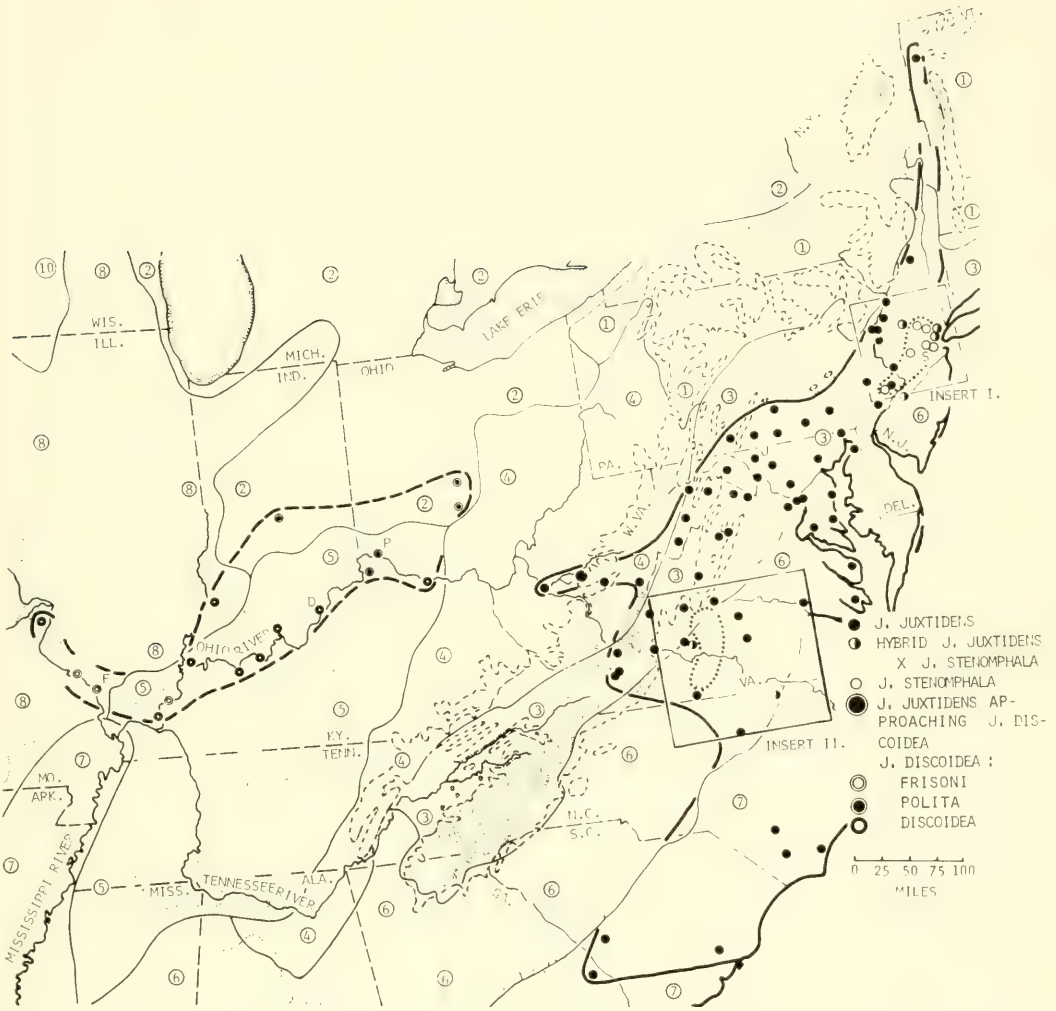


Figure 9. Distribution of *Triodopsis juxtidens*. Thick solid line surrounds the range of *j. juxtidens;* thick, dashed line, *j. discoidea;* dotted line, *j. stenomphala.* D, type locality of *j. discoidea;* F, *frisoni;* J, *j. juxtidens;* P, *polita;* S, *j. stenomphala.* Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3. The two inserts are shown in Figure 10.

leys, and one of *T. rugosa*, via the Holston and French Broad, and Yadkin and Catawba valleys (Figs. 3, 7). Speaking in phytogeographic terms, the valleys are "straits" of deciduous forests between "islands" of coniferous forests that cover the peak regions (Fig. 19). The straits are evidently favorable for the passing of snails adapted to the deciduous forests.

The *measured material* comes from the following localities: *Vermont*: Chittenden County (MCZ). *Pennsylvania*: Pike and Lancaster counties (MCZ); Monroe, Northampton, Bucks, and Philadelphia counties (ANSP). *New Jersey*: Sussex and Warren counties (MCZ). *Maryland*: Washington and Baltimore counties (ANSP); Charles County (MCZ). *West Virginia*: Jefferson County (ANSP); Nicholas and Kanawha counties (CM). *Virginia*: Shen-

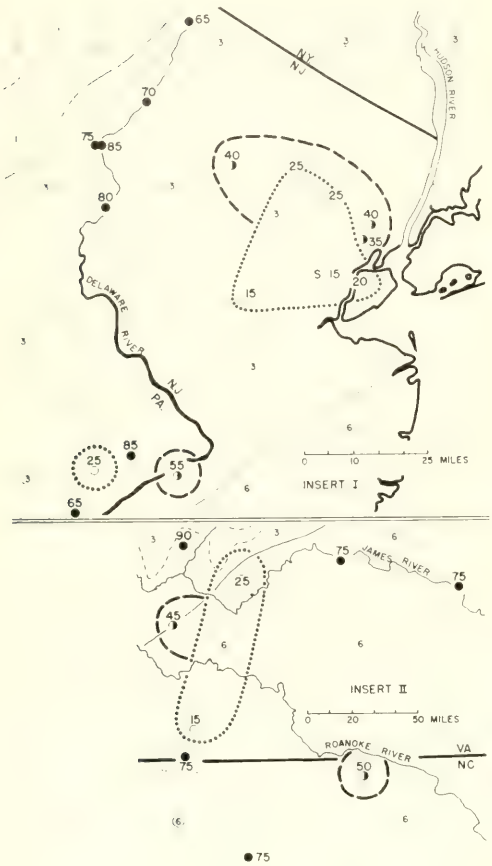


Figure 10. Inserts to Figure 9; detailed distribution of *Triodopsis j. stenomphala*, hybrid *j. stenomphala* × *j. juxtidens*, and adjacent populatons of *j. juxtidens*. Thick, dashed line surrounds the range of the hybrids, dotted line, *j. stenomphala*. Numbers without a circle are mean values of samples in character index; samples of *j. stenomphala* range from 15–30; hybrid, 35–55; *j. juxtidens*, 60–90 (samples of the latter species also occur in areas not covered by the inserts). Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3, except that the state lines are marked with thick, solid lines.

andoah, Rockbridge, Warwick, and Pittsylvania counties (ANSP); Fairfax, Northumberland, Buckingham, and Henrico counties (MCZ). *Washington, D.C.*: Zoological Park (MCZ). *North Carolina*: Durham, Bladen, and New Hanover counties (ANSP); Columbus County (MCZ). *South Carolina*: Aiken and Orangeburg counties (ANSP). A total of 30 samples, 1–32 specimens each, 248 specimens altogether.

Ecology. Triodopsis j. juxtidens occurs in northern hardwoods, mixed mesophytic, oak-chestnut, oak-pine and southeastern evergreen forests, between sea level and 2000 feet (Fig. 9). It is often found on riverbanks (Hubricht, 1950b; own experience).

Triodopsis j. juxtidens slightly overlaps the related species *T. tridentata*. Pilsbry states (1940: 799) that in the zone of overlap "in any suitable place either *tridentata* or *juxtidens* is to be found, but never the two together, in my experience; however, A. F. Archer reports finding them together at Lambertville, New Jersey." My experiences in New Jersey and Pennsylvania seem to verify Pilsbry's observations. The two species probably have very similar ecological requirements; therefore they cannot coexist in the same habitat for a long period of time. This is another example of ecological exclusion.

Triodopsis j. juxtidens probably shows habitat exclusion with *T. f. fallax* and *f. obsoleta*, also. More collecting should be done, however, to more firmly establish this observation.

Variation. The various elements of the *aperture*, such as the lip swelling, lip teeth, parietal lamella and outline of the whole aperture, vary irregularly through the greater part of the range of the species. Some regularity can be observed, however. Thus, at the southern end of the range, most specimens have an aperture almost circular in outline, evenly and deeply receding lip swelling and lip teeth (dish-like aperture), and a long parietal lamella. In marshy areas most specimens have a normal aperture with a nearly straight parietal lamella. Neither of these groups qualifies as a subspecies; the first group occurs in too limited an area and is too weakly characterized, the second group is primarily an ecological form.

Of the *measured characters*, width of shell is correlated with height, umbilicus

and whorl number. All measured characters show irregular geographic variation.

The variation of the character index is discussed in a later section.

Systematics. Triodopsis j. juxtidens was formerly considered a subspecies of *T. tridentata*. It should be considered, however, distinct from it. It maintains its identity even in areas where it overlaps *tridentata*, demonstrating its reproductive isolation from that form. Previous authors who combined them in one species overlooked this.

Triodopsis juxtidens stenomphala subsp. n. Plate II: 7–9

Holotype: MCZ 18159a. Acquired from the Bland Collection, collector and date of collecting not known. *Paratypes*: MCZ 18159b; other data as above. The name *stenomphala*, meaning "of narrow umbilicus," expresses an outstanding feature of the new form.

Type locality: Rahway, Union County, New Jersey.

Definition. Triodopsis j. stenomphala contains those populations of the species having mean values of 15–30 in character index. (The method of computing character index is shown in Table II.)

Description. Shell width 9.8–13.5 mm; height 5.6–7.8 mm, height to width ratio 0.50–0.59; umbilicus 1.1–1.8 mm, umbilicus to width ratio 0.39–0.49; embryonic whorls and sculpture as in *j. juxtidens*, except for a reduction in number of granules; aperture square; lip swelling well developed and nearly marginal, so that edge of peristome is slightly swollen; lip teeth moderately large, upper lip tooth slightly receding, lower lip tooth marginal; parietal lamella large, long, and nearly straight, pointing above upper lip tooth.

Differential diagnosis. Triodopsis j. stenomphala differs from *j. juxtidens* in having a narrower umbilicus, a tighter coiling of the whorls, and a larger and longer parietal lamella. Other, less important diagnostic features are the smaller dimensions of the shell and the squarish, swollen aperture. The marsh-dwelling populations of *j. juxtidens* may be very hard to separate from *j. stenomphala*, since they are also small and have long, straight parietal lamellae.

Distribution. Triodopsis j. stenomphala has a disjunct distribution. It occurs in three small areas in New Jersey, Pennsylvania, and Virginia (Figs. 9, 10), the first two of these possibly being connected. In New Jersey and probably in Pennsylvania it is allopatric with *j. juxtidens*; in Virginia, it is "sympatric," although not coexistent. According to Hubricht, the two forms occupy different habitats in Virginia (see below).

The Virginian occurrence is possibly of recent origin. Perhaps lumber trucks are responsible, as suggested by R. T. Abbott (personal communication, 1962). There is no great need, however, to involve human agencies. The snail could have gotten to Virginia by natural means such as "walking," by being carried by rivers, winds or birds; also, it could be a relict of earlier times, like *T. pendula*. Still another possibility is to assume that the New Jersey—Pennsylvania population evolved independently of the Virginia population; in other words, to assume that *j. stenomphala* is a polytopic subspecies. This seems to me unlikely, however, since the two populations live in different habitats, whereas the populations of a polytopic subspecies are supposed to occur in "identical" habitats. The best explanation would appear to involve natural dispersal and recent origin. At any rate, the Virginia population presently forms a geographic isolate of the New Jersey-Pennsylvania population.

The *measured material* comes from the following localities: *New Jersey*: Morris County (ANSP); Essex, Union, and Somerset counties (MCZ). *New York*: Richmond County (MCZ). *Virginia*: Amherst and Pittsylvania counties (ANSP). A total of 8 samples, 2–8 specimens each, 34 specimens altogether.

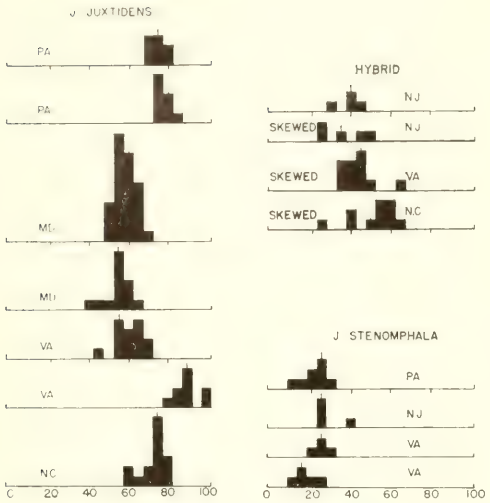


Figure 11. Character index histograms of samples of *Triodopsis j. juxtidens, j. stenomphala,* and hybrids between the two subspecies. Short line on top of column indicates mean value of sample. The histograms of most hybrid samples are strongly skewed, those of the parental forms slightly skewed or normal. The abbreviations stand for the states where the samples have been collected. Scale in character index units.

Ecology. In the New Jersey-Pennsylvania area, *T. j. stenomphala* is found on both low and high ground. In Virginia, however, it ". . . is common in upland oak woods in the Outer Piedmont," whereas on the river bluffs another form, *j. juxtidens*, is abundant (Hubricht, 1950b). Thus it seems that in the New Jersey-Pennsylvania area the subspecies occupies a wider range of habitats than in Virginia. In view of the fact that in the former area no related form occurs, whereas in the latter area *j. juxtidens* is present, we may assume that the restriction to the uplands is caused by the presence of, or more specifically, the competition provided by, the related form, which is superior on the river bluffs. The situation is very complex, however. *Triodopsis j. stenomphala* and *j. juxtidens* not only seem to compete but also to hybridize with each other. This, of course, cannot go on indefinitely. If hybridization continues, the two forms will merge. If the hybrids are of reduced viability, hybridization will cease, and each group will be restricted to a single kind of habitat, either upland or lowland.

A similar situation can be observed in *T. complanata.* There, too, one subspecies has a broader and the other a narrower ecological range, and the latter is "sympatric" with the related form, *T. tridentata.* Interestingly, in both cases, the subspecies with the smaller population size has the evolutionarily more advanced, narrower (more specialized) range. This may be because a population of small size may reorganize its genetic constitution more rapidly than a population of large size (Mayr, 1954; 1963: 527); such reorganization is probably necessary for changing the ecological range.

Systematics. Triodopsis j. stenomphala is sufficiently distinct to be recognized as a taxonomic unit. This was shown in the description and differential diagnosis. It cannot be considered a full species, however, because it freely interbreeds with *j. juxtidens.* The evidence for this is discussed below.

Hybrid populations between *Triodopsis j. juxtidens* and *j. stenomphala*

Plate II: 4–6

Some populations of *Triodopsis juxtidens* are intermediate between the two subspecies according to their character index; they have mean values of 35–55, as compared to 15–30 for *j. stenomphala* and 60–90 for *j. juxtidens.* These populations are considered to be of hybrid origin for the following reasons. First, they show a greater variation than the "pure" populations of either *j. juxtidens* or *j. stenomphala*, as demonstrated by comparison of their character index histograms (Fig. 11), or of the range of variation (Fig. 4). Second, these populations are found in the zone of contact between the two subspecies (Figs. 9 10).

Attention should be called to the fact that the character index histograms of most hybrid populations are skewed (Fig. 11).

The same phenomenon, though even more pronounced, can be observed in the hybrids of *T. f. alabamensis* with *f. fallax* and *f. obsoleta* (Fig. 18). A skewed distribution curve is not a necessary criterion of hybrid origin, and it may only be accidental that in *Triodopsis* so many hybrid populations have this attribute. The phenomenon is best explained by the introduction of one or a few specimens of parent A into a population of parent B with subsequent maintenance of the resulting imbalance.

Hybrid samples have been *measured* from the following localities: *New Jersey*: Burlington, Hudson, and Essex counties (MCZ); Morris County (ANSP). *Virginia*: Bedford County (MCZ). *North Carolina*: Warren County (ANSP). A total of 6 samples, 1–12 specimens each, 35 specimens altogether.

In New Jersey, the hybrid populations live both in the hills and on the riverbanks, just as the parent populations do. I do not have enough information on the habitat of the hybrids living in the Virginia area.

The occurrence of hybrid populations is important taxonomically, because it proves the conspecificity of what are called here *j. juxtidens* and *j. stenomphala*.

Triodopsis juxtidens discoidea (Pilsbry) Plate II: 10–11

Polygyra tridentata subsp. *discoidea* Pilsbry, 1904, Nautilus 17: 142. Charlestown Landing, Clark County, Indiana. Type ANSP 11076.

H(elix) tridentata subsp. *polita* Wetherby, 1894, Nautilus 8: 44. Limestone cliffs above Cincinnati, Hamilton County, Ohio. Not *Helix polita* Pulteney, 1797, or Mueller, 1774. Type ANSP 98940.

Polygyra tridentata var. *frisoni* F. C. Baker, 1933, Nautilus 47: 58. South end of Fountain Bluff, Jackson County, Illinois. Paratypes ANSP 161146.

Definition. *Triodopsis j. discoidea* corresponds to *T. tridentata discoidea* of Pilsbry (1940). A character index was not prepared for this taxon.

Description. Shell width 12.9–20.9 mm; height 5.8–10.0 mm, height to width ratio 0.40–0.54; umbilicus 2.2–4.6 mm, umbilicus to width ratio 0.14–0.23; embryonic whorls 1.4–1.5, faintly or definitely striated below suture, smooth otherwise; striation becoming more pronounced on subsequent whorls, 3–5 striae per millimeter on last whorl; striae from very low to moderately high, their intervals almost smooth, or with fine or pronounced granules; aperture trapezoid to oval-triangular; lip swelling and lip teeth well developed, somewhat receding; upper lip tooth usually broad and flat; upper and lower teeth close to each other; parietal lamella moderately developed, arcuate, pointing slightly above upper lip tooth.

Differential diagnosis. *Triodopsis j. discoidea* differs from *j. juxtidens* by its larger and flatter shell, which is often smooth and shiny, flatter aperture, and wider umbilicus. From *T. tridentata* it differs in various apertural features; the lip teeth are in close proximity, the distance between them being much less than the distance that separates the upper lip tooth from the junction of the upper lip with the shell; the upper lip tooth is broad and slightly receding, with the parietal lamella pointing above it; the shell is flat and the umbilicus is wide. In contrast, the lip teeth of *tridentata* are farther from each other, the upper lip tooth is not broad or receding, the parietal lamella points at or below it, the shell is higher and the umbilicus narrower.

Distribution. *Triodopsis j. discoidea* occurs in the Ohio and the Mississippi valleys (Fig. 9). Its range is partially separated from that of its closest ally, *j. juxtidens*, by the Appalachian Mountains. The separation was once more complete, but has broken down in the Kanawha River valley in recent times (p. 166).

The *measured material* comes from the following localities: *Ohio*: Franklin, Brown, and Hamilton counties (2 samples, both

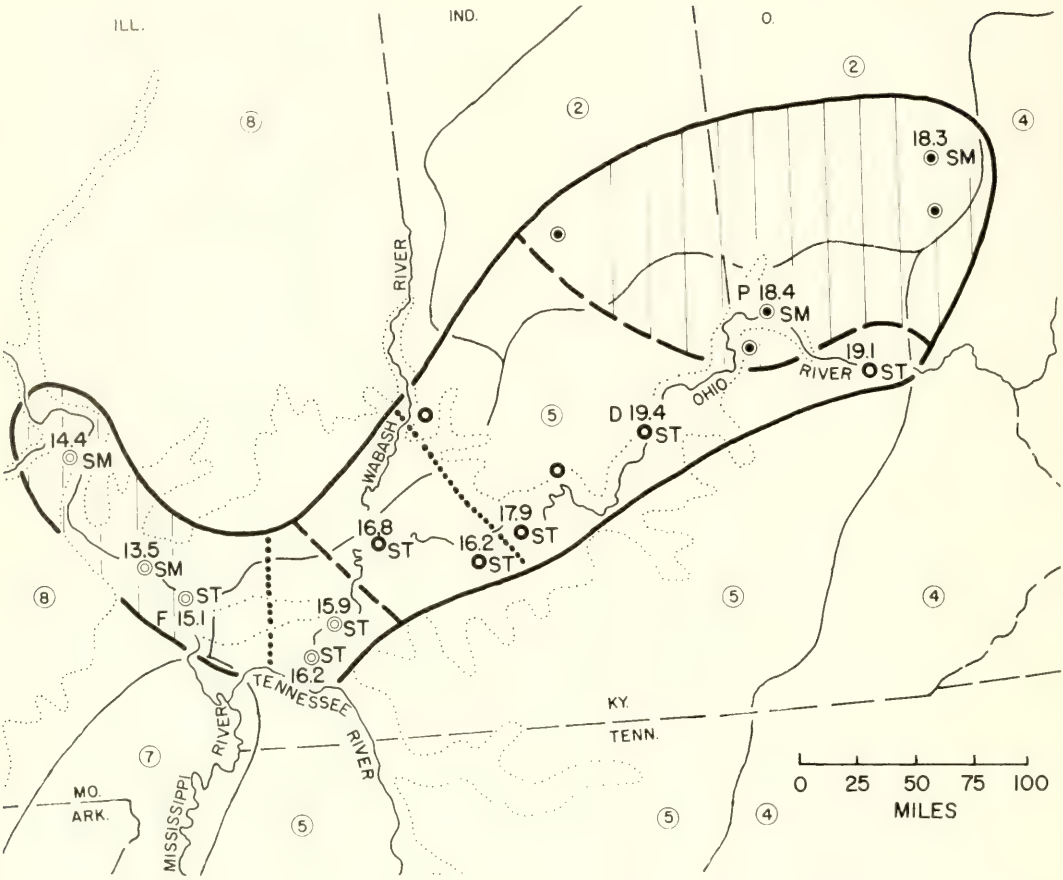


Figure 12. Geographic variation of size (shell width) and sculpture in *Triodopsis j. discoidea*. Thick, solid line surrounds the range of the subspecies; thick, dashed line separates *polita*, *discoidea*, and *frisoni*, all included in *j. discoidea*; dotted line separates the samples with small size, 13.5–15.1 mm, from intermediate, 15.9–16.8, and large, 17.9–19.4. The size shows a gradual increase from the west to the east; the sculpture does not. Thus, the two characters vary discordantly. SM, smooth sculpture; ST, striated sculpture. Other symbols as in Figure 9.

ANSP). *Indiana*: Perry, Posey, and Clark counties (ANSP). *Illinois*: Randolph, Jackson, Pope, and Hardin counties (ANSP). *Kentucky*: Davies County (MCZ). *Missouri*: St. Louis County (ANSP). A total of 13 samples, 3–15 specimens each, 94 specimens altogether.

Ecology. Triodopsis j. discoidea is largely confined to the valleys of two major rivers, the Mississippi and the Ohio. It seems to prefer the immediate vicinity of the rivers, according to various collectors who have found it on river banks or on cliffs near the rivers. The area is covered by beech-maple, oak-hickory and western mesophytic forests. It lies between 300 and 500 feet (Fig. 9).

Pilsbry (1940: 800) quotes Daniels as saying that in Indiana *T. j. discoidea* "occurs on the immediate banks of the Ohio River, but when you go back into the country you get the typical *tridentata*." If so, this is another example of habitat exclusion. We can assume that *j. discoidea* and *tridentata* once had broader and overlapping ecological spectra, and therefore were

competing with each other. In time, however, *j. discoidea* became adapted to the more humid habitats, while the *tridentata* populations of the area became adapted to the drier habitats. This resulted in the habitat exclusion that can be observed at present. The advantage of this arrangement is that it reduces direct competition between the two forms. A similar arrangement exists between *T. c. platysayoides* and *T. tridentata*, and between *j. juxtidens* and *j. stenomphala*.

Plant associations apparently play no direct role in determining the distribution of the subspecies. This is evidenced by the lack of correlation between the subspecies border and the boundaries of the plant associations in the area (Fig. 9).

Variation. The *sculpture* varies from smooth to striated. The former condition is usually associated with moist habitats, as in the case of *c. complanata*. It is not definitely known whether this character has a genetic basis or is a purely environmental modification, but as not all shells from moist habitats are smooth, the former assumption is apparently correct.

Measured characters: Shell width is correlated with height and umbilicus. The shell width increases clinally from west to east (Fig. 12), one of the few instances of this phenomenon in *Triodopsis*. The height to width, and umbilicus to width ratios show irregular geographic variation.

It should be pointed out that sculpture and shell width vary discordantly. The sculpture changes from smooth to striated and back to smooth from east to west, whereas the width grades from small to large in the same geographic sequence. It follows that neither these characters nor their combinations can serve as key taxonomic characters, although they have been used as such in the past.

Systematics. Triodopsis j. discoidea was formerly considered a subspecies of *T. tridentata*. In fact, however, it is specifically separate from that form, since it is reproductively and ecologically isolated from it. Reproductive isolation may be inferred from the discontinuity between the two forms in certain morphological features, which exists in spite of their "sympatric" distribution. These features were listed previously. It is clear that were *j. discoidea* and *tridentata* conspecific, such discontinuities would not exist. The occurrence of ecological isolation was discussed in the section above.

The very same characters that separate *discoidea* from *tridentata* connect *discoidea* with *juxtidens* (see Plates I and II, and the descriptions of the two forms). The only question is whether *discoidea* should be ranked as a subspecies of *juxtidens* or whether it should be treated as a separate species. On the assumption that they would interbreed should they come in contact, we will consider them conspecific. This assumption is justified, since intergrading populations between the two forms occur. On the above basis, the name *T. tridentata discoidea* should be changed to *T. juxtidens discoidea*.

Under the name *discoidea*, Pilsbry combined three taxa: *discoidea*, *polita*, and *frisoni* (1940: 800). I agree with this action. It is true that the three forms differ slightly in sculpture and size, *polita* being large and smooth, *discoidea* medium to large and striated, and *frisoni* medium to small and smooth or striated. But the variation in size and sculpture is gradual and discordant, so that a classification based upon size and sculpture variations would not be valid.

Triodopsis j. juxtidens population approaching *j. discoidea*

A population of *j. juxtidens*, collected in the valley of the Kanawha River, Clay County, West Virginia (CM: 5 specimens), consists of shells which are larger and flatter, and which have a flatter aperture than do those of normal *j. juxtidens*. They clearly approach *j. discoidea* in these characters. They are not smooth, however, as *j. discoidea* usually are, but striated and

Table III

Measurements of the Clay County *j. juxtidens* Population. For Comparison, the Measurements of Representative *j. juxtidens* and *j. discoidea* Populations are Also Shown. The Clay County Population Apparently Occupies an Intermediate Position Between *j. juxtidens* and *j. discoidea*.

Name	Remark	Locality	Number of Specimens	Mean of			Sculpture
				width in mm	height to width ratio	umbilicus to width ratio	
j. juxtidens		West Virginia, near the Clay County population	1	15.5	0.52	0.16	striated
j. juxtidens	second largest in subspecies	Virginia	9	17.1	0.51	0.16	striated
j. juxtidens	widest umbilicus in subspecies	West Virginia	2	14.8	0.52	0.18	striated
j. juxtidens approaching *j. discoidea*		Clay County, West Virginia	5	18.5	0.49	0.17	striated
j. discoidea	easternmost *j. discoidea*	Ohio	5	19.1	0.47	0.18	striated
j. discoidea		Ohio	3	18.3	0.49	0.19	smooth
j. discoidea	largest with widest umbilicus in subspecies	Indiana	6	19.4	0.43	0.21	striated

have a narrow umbilicus, as in *j. juxtidens* (Table III). These specimens are apparently intergrading between *j. juxtidens* and *j. discoidea*; I call them *j. juxtidens* only because they are found within the range of this subspecies, and the range of *j. discoidea* starts 110 miles farther west (Fig. 9).[1]

As far as the origin of this population is concerned, there are two possibilities. It might have arisen through interbreeding of the two subspecies, or it might have developed from the local *j. juxtidens* population, under local selection pressure. Since only one small population is involved, statistical methods were not employed to select the right answer. Judging from simple inspection of the material, though, the range of variation seems normal, which supports the second interpretation.

Whichever interpretation is true, the occurrence of an intergrading population indicates the conspecificity of *j. juxtidens* and *j. discoidea*. The first interpretation would indicate that interbreeding actually took place. The second would indicate a great similarity between the two gene pools, and thus the possibility of interbreeding should the two forms come in contact.

Evolutionary relationships. Among the three members of the *juxtidens* complex, *j. juxtidens* approaches the hypothetical ancestor of *Triodopsis* most closely, inasmuch as it has a striated shell and an unspecialized, broad ecological spectrum. That *j. discoidea* is evolutionarily more advanced than *j. juxtidens* is indicated by its smooth shell and specialization for a particular habitat (p. 172). *Triodopsis j. stenomphala* does not have these traits. It is considered a descendant of *j. juxtidens* because it appears to be a geographical isolate

[1] In the spring of 1967 the author and Mr. Paul Blachman collected populations apparently intermediate between *Triodopsis j. juxtidens* and *j. discoidea* at several other localities as well (Bladen, Gallia Co., Athalia and Coal Grove, Lawrence Co., Ohio; Ghent, Carroll Co., Ky.; on the banks of the Ohio River). Furthermore, they found that these populations do not interbreed with *T. j. juxtidens* at all, whereas they interbreed freely with *T. tridentata*. Thus the morphological resemblance of these populations to *T. j. juxtidens* and *T. j. discoidea* has proved to be deceptive.

of that form. It probably developed from a New Jersey *juxtidens* population which was separated from the main population by the Delaware River valley.

The *juxtidens* complex occupies a morphologically intermediate position between the *tridentata* and *fraudulenta* complexes. But nothing is known as to when and under what circumstances the three taxa separated.

Summary. (1) *Triodopsis juxtidens* consists of three subspecies, *j. juxtidens*, *j. stenomphala*, and *j. discoidea*, and of hybrids and intermediates connecting them. The typical subspecies was formerly considered a subspecies of *T. tridentata*; *j. stenomphala* is a new form, formerly included in *j. juxtidens*; *j. discoidea* is the former *T. tridentata discoidea*, including the former *t. polita* and *t. frisoni* as synonyms.

(2) The range of *j. stenomphala* is separated from that of *j. juxtidens* by a hybrid belt. A few populations of *j. stenomphala* "overlap" *j. juxtidens*, also with hybridization. *Triodopsis j. discoidea* is entirely allopatric with *j. juxtidens*. One of the westernmost populations of *j. juxtidens* morphologically approaches *j. discoidea*.

(3) *Triodopsis j. juxtidens* and *j. stenomphala* occupy all available habitats when they are allopatric, but in areas of "sympatric" occurrence, *j. juxtidens* is confined to river banks and *j. stenomphala* to the uplands. Thus the two forms do not coexist, and thereby demonstrate the exclusion principle. *Triodopsis j. discoidea* occurs only in large river valleys, mainly on the river banks. Both *j. juxtidens* and *j. discoidea* show exclusion with *T. tridentata*, and the former also with *T. f. fallax* and *f. obsoleta*.

(4) The geographic variation is generally irregular in all three subspecies. Exceptions are the clinal variation of the shell width (size) in *j. discoidea* and possibly that of the parietal lamella in *j. juxtidens* and the sculpture in *j. discoidea*, which may be correlated with wetness of the habitat.

(5) The combination of *juxtidens, stenomphala* and *discoidea* in one species is justified by the fact that hybrids or intergrades occur between them. The taxon thus formed is specifically distinct from *tridentata*, as the two appear to be reproductively isolated.

The *fraudulenta* Complex

Definition. This complex contains four taxa: *Triodopsis fraudulenta*, *T. pendula*, and two subspecies of *T. neglecta—n. vulgata* and *n. neglecta*. *Triodopsis fraudulenta* is definitely a distinct species, *T. pendula* is probably so; *T. n. vulgata* and *n. neglecta* are probably conspecific. The central stock from which the other three taxa are derived is *n. vulgata*; therefore the discussion will begin with this taxon.

Triodopsis neglecta (Pilsbry)
Triodopsis neglecta vulgata (Pilsbry)
Plate II: 12–14

Triodopsis fraudulenta subsp. *vulgata* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 805, fig. 478b,c. Columbus, Franklin County, Ohio. Type ANSP 57148.

Triodopsis hopetonensis subsp. *claibornensis* Lutz, 1950, Nautilus 63: 121, fig. 1. Foothills of the Cumberland Mountains near the Grace Nettleton Home for Girls, Harrogate, Claiborne County, Tennessee. Paratype ANSP 215860.

Definition. Triodopsis n. vulgata combines the former *T. fraudulenta vulgata* and *T. hopetonensis claibornensis*. It contains those populations of the *fraudulenta* complex which have mean values of 50–75 in character index (Table IV).

Description. Shell width 12.2–19.8 mm, height 5.8–10.6 mm, height to width ratio 0.41–0.63; umbilicus 2.4–5.1 mm, umbilicus to width ratio 0.16–0.30; number of whorls 5.0–6.4, whorl to width ratio 0.30–0.45; upper tooth to lower tooth ratio 1.00–1.29; embryonic whorls 1.3–1.4, finely striated below suture; striation on later whorls becoming more pronounced, 3–4 striae per millimeter on last whorl; space between striae with papillae or fine spiral lines,

Table IV

Chart for Computing Character Index of *Triodopsis n. vulgata*, *n. neglecta*, and *T. pendula*. Method of Calculation: a Shell with a Width of 19.3 mm, a Height of 10.5 mm, an Upper Tooth to Lower Tooth Ratio of 0.99, a Whorl to Width Ratio of 0.30, and an Umbilicus to Width Ratio of 0.15 was Scored $(70 + 65 + 65 + 50 + 50)/3 = 100$, Maximum Available Score.

Score	Width	Height	Upper to lower tooth ratio	Whorl to width ratio	Umbilicus to width ratio	
0	9.9–10.5	3.5–4.0	1.39–1.42	0.50–0.51	0.29–0.30	*n. neglecta*
5	10.6–11.2	4.1–4.5	1.35–1.38	0.48–0.49	0.27–0.28	↑
10	11.3–11.9	4.6–5.0	1.32–1.34	0.46–0.47	0.26	
15	12.0–12.6	5.1–5.5	1.29–1.31	0.44–0.45	0.25	
20	12.7–13.3	5.6–6.0	1.26–1.28	0.42–0.43	0.24	
25	13.4–13.9	6.1–6.5	1.23–1.25	0.40–0.41	0.23	
30	14.0–14.5	6.6–7.0	1.20–1.22	0.38–0.39	0.22	
35	14.6–15.1	7.1–7.5	1.17–1.19	0.36–0.37	0.21	*pendula*
40	15.2–15.7	7.6–8.0	1.14–1.16	0.34–0.35	0.19–0.20	
45	15.8–16.3	8.1–8.5	1.11–1.13	0.32–0.33	0.17–0.18	
50	16.4–17.0	8.6–9.0	1.08–1.10	0.30–0.31	0.15–0.16	
55	17.1–17.7	9.1–9.5	1.04–1.07			
60	17.8–18.4	9.6–10.0	1.00–1.03			
65	18.5–19.1	10.1–10.6	0.96–0.99			
70	19.2–19.8					↓ *n. vulgata*

umbilical region and shoulder of last whorl always with papillae; aperture square, dished; lip swelling thick; upper lip tooth broad and receding, located on right side of aperture; lower lip tooth medium large and marginal, located at or near middle of lower lip; parietal lamella of normal size, nearly straight.

Differential diagnosis. Triodopsis n. vulgata differs from *T. j. juxtidens* in that the upper lip tooth is broader and more receding, the whorls are more capacious, and the umbilicus is wider and more cylindrical. It is distinguished from *T. f. fallax* by its wide and cylindrical umbilicus, capacious whorls, and straight parietal lamella.

Distribution. Triodopsis n. vulgata occurs in a vast area from Ontario south to Alabama, and from the Mississippi River east to the Appalachian Mountains (Fig. 13). Isolated outposts occur in eastern Wisconsin, New York, Maryland, and North Carolina.

The *measured material* comes from the following localities: *Ontario*: Elgin County (ANSP); Essex County (MCZ). *Michigan*: Oakland, Wayne, and Washtenaw counties (ANSP); Ionia County (MCZ). *Washington, D. C. Virginia*: Lee County (ANSP). *West Virginia*: Ohio County (ANSP); Hampshire County (MCZ). *Ohio*: Guernsey, Erie, Franklin, Cuyahoga, Warren, and Adams counties (ANSP); Hamilton County (MCZ). *Indiana*: Dearborn and Crawford counties (ANSP); Kosciusko, Tippecanoe, and Marion counties (MCZ). *Illinois*: Gallatin County (MCZ). *Kentucky*: Trimble and Casey counties (MCZ). *North Carolina*: Cabarrus and Clay counties (ANSP); Knox, Monroe, and Jackson counties (MCZ). *Alabama*: Madison (2 samples) and Jackson counties (ANSP). A total of 37 samples, 1–25 specimens each, 231 specimens altogether.

Ecology. Triodopsis n. vulgata is widely distributed in the beech-maple and western mesophytic forests. It also penetrates the periphery of the oak-chestnut, mixed mesophytic and oak-pine forest regions (Fig. 13). The northern limits of its range more or less coincide with those of the beech-maple forests. The plant association may be the factor that determines the subspecies border.

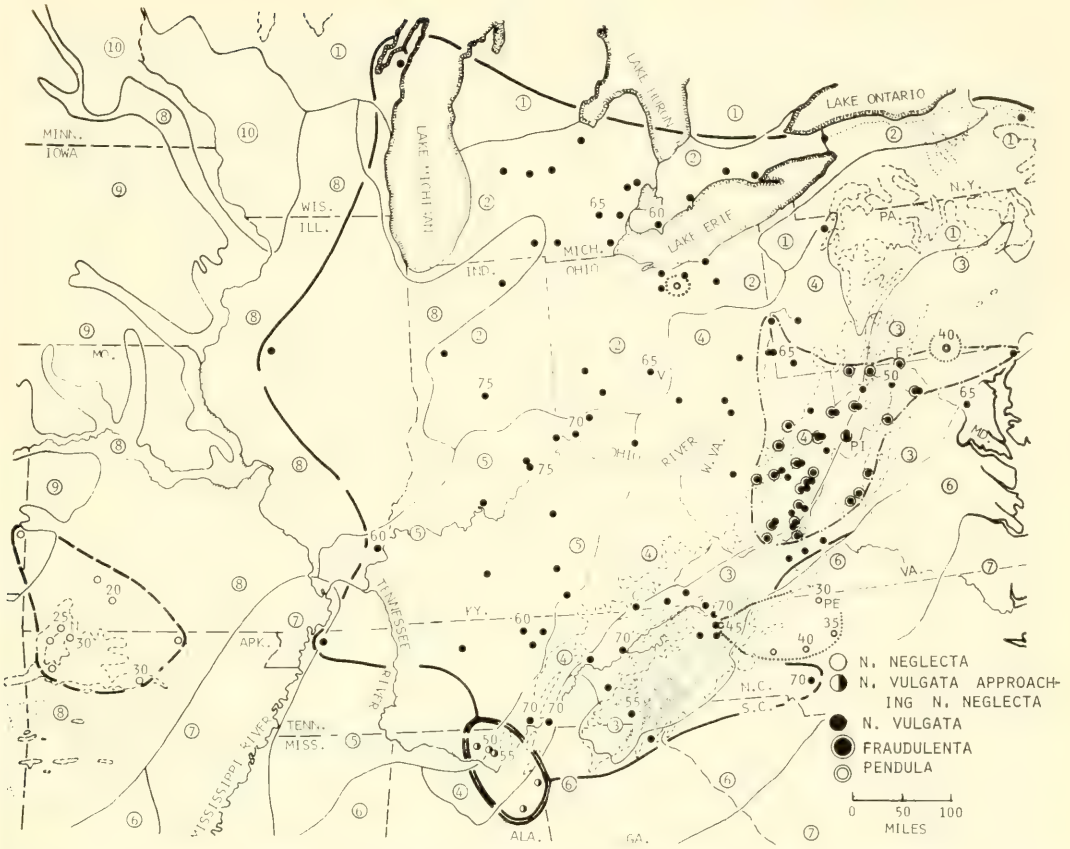


Figure 13. Distribution of *Triodopsis fraudulenta, neglecta,* and *pendula,* and the geographic variation of the character index in *neglecta* and *pendula.* Thick, solid line surrounds the range of *n. vulgata;* double, thick, solid line, *n. vulgata* approaching *n. neglecta;* thick, dashed line, *n. neglecta;* dotted line, *pendula;* dash-dot, *fraudulenta.* C, type locality of *claibornensis,* considered synonymous with *n. vulgata;* F, *fraudulenta;* N, *n. neglecta;* PE, *pendula;* PI, *picea,* considered synonymous with *fraudulenta;* V, *n. vulgata.* Numbers without a circle are mean values of samples in character index; samples of *n. neglecta* range from 20–30; *n. vulgata* approaching *n. neglecta,* 50–55; *n. vulgata,* 50–75; *pendula,* 30–40. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Most localities occur between 500 and 1500 feet (Fig. 13), but some lie at much lower or much higher elevations. Thus, one sample from Washington, D. C., comes from near sea level, another, from the Roan Mountains, Carter County, Tennessee, from 4000–5000 feet. Such high records are rare, however; on the whole, the subspecies does not seem to ascend as high as *T. fraudulenta* or *T. tridentata.*

Variation. The *aperture* varies only moderately. The separation of aperture grades, therefore, was not necessary.

Sculpture: The surface of the shell between the striae is covered with papillae. Fine spiral lines may replace the papillae on portions of the last whorl, but the umbilical and shoulder regions are always papillate. The papillae and the spiral lines intergrade; therefore, they can be considered homologous structures. The sculpture of *T. rugosa* shows similar intergradation.

Among the *measured characters,* shell width is correlated with height, umbilicus, and whorl number, not with the upper tooth to lower tooth ratio. All characters

TABLE V

MEASUREMENTS OF *TRIODOPSIS H. CLAIBORNENSIS*, AND OF REPRESENTATIVE POPULATIONS OF *T. N. VULGATA* AND *T. F. OBSOLETA*. THE ARROWS POINT TOWARD THE TAXON TO WHICH *CLAIBORNENSIS* SHOWS THE GREATER SIMILARITY IN THE CHARACTER IN QUESTION. BECAUSE OF THESE SIMILARITIES, AND ALSO BECAUSE OF ITS DISTRIBUTION, *CLAIBORNENSIS* IS CONSIDERED SYNONYMOUS WITH *N. VULGATA*.

			Mean of				
Name	Locality	Number of specimens	Width in mm	Height to width ratio	Umbilicus to width ratio	Whorl to width ratio	Upper to lower tooth ratio
n. vulgata	N. Carolina	6	13.5	0.51	0.21	0.40	1.15
n. vulgata types	Ohio	5	13.5	0.54	0.22	0.36	1.10
h. claibornensis type	Tennessee	1	12.7	0.54	0.19	—	1.20
f. obsoleta	N. Carolina	25	10.8	0.56	0.14	0.47	—
f. obsoleta	S. Carolina	5	11.4	0.54	0.15	0.47	1.20–1.25

show irregular geographic variation. It is remarkable that a form as widely distributed as *n. vulgata* has not developed any cline.

The mean values of population in character index also show moderate and irregular geographic variation (Fig. 13). All this evidence indicates that *n. vulgata* shows primary intergradation.

Systematics. Triodopsis n. vulgata is a widespread, common snail. Yet it somehow escaped description until as late as 1940. The partial reason for this delay may be that its conspecificity with a related form, *T. fraudulenta*, was taken for granted, and thus the workers could refer to it as *fraudulenta*; but the whole reason remains obscure to me. Northern and southern populations of *tridentata* were not named either, although one would have expected it because of their dissimilarity (p. 156).

As will be shown in later sections, *vulgata* is specifically distinct from *T. fraudulenta*, and probably conspecific with *T. neglecta*. For these reasons, and since *neglecta* is an older name than *vulgata*, it is necessary to change its name to *T. neglecta vulgata*.

Small, depauperate specimens of *T. n. vulgata* from Harrogate, Claiborne County, Tennessee, have been described by Lutz (1950) as *T. hopetonensis claibornensis*. They are not *hopetonensis*,[1] however, but *T. n. vulgata*, as shown by the comparison of some measurements (Table V). Also, *f. obsoleta* (= *hopetonensis*) does not occur anywhere near Harrogate, whereas *n. vulgata* does.

Triodopsis neglecta neglecta (Pilsbry) Plate II: 18–20

Polygyra neglecta Pilsbry, 1899, Nautilus 13: 40. Eureka Springs, Carroll County, Arkansas. Type ANSP 76283.

Triodopsis fallax Say, var. *minor* Wetherby, 1881, J. Cincinnati Soc. Nat. Hist. 4: 333. Springfield, Greene County, Missouri. *Non T. introferens* var. *minor* Tryon, 1867. Type not seen.

Definition. Triodopsis n. neglecta corresponds to *T. neglecta* of earlier authors. It contains those populations of the *fraudulenta* complex which have mean values between 20 and 30 in character index. The character index was prepared as shown in Table IV (p. 176).

Description. Shell width 9.9–13.2 mm, height 4.6–6.5 mm, height to width ratio 0.41–0.53; umbilicus 2.1–3.9 mm, umbilicus to width ratio 0.20–0.30; number of whorls 4.8–6.0, whorl to width ratio 0.40–0.51; upper tooth to lower tooth ratio 1.08–1.46;

[1] *Triodopsis hopetonensis* is considered hybrid between *T. f. alabamensis*, *f. fallax*, and *f. obsoleta* (p. 198). The taxon which Lutz called *hopetonensis* is here called *f. obsoleta* (p. 187).

embryonic whorls and sculpture as in *n. vulgata*; aperture square to trapezoid; lip swelling, lip teeth, and parietal lamella of moderate size; parietal lamella angular, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis n. neglecta* differs from *T. n. vulgata* in that the shell is smaller, flatter, and more tightly coiled, the umbilicus wider and more cylindrical, the parietal lamella more angular, and the upper tooth to lower tooth ratio higher.

Distribution. *Triodopsis n. neglecta* occurs in the foothills of the Ozark Mountains, in Missouri and Arkansas. It is a peripheral isolate of *n. vulgata*, being separated from the latter by the Mississippi Valley (Fig. 13). There is a gap of about 150 miles between the closest *n. neglecta* and *n. vulgata* localities. The intervening area is not well collected, however, and new localities in this area may be discovered.

The *measured material* comes from the following localities: *Missouri*: Greene, Barry, and Christian counties (ANSP). *Arkansas*: Washington, Benton, Carroll, and Searcy counties (ANSP). *Kansas*: Bourbon County (2 samples). A total of 9 samples, 1–30 specimens each, 81 specimens altogether.

Ecology. *Triodopsis n. neglecta* is largely confined to the oak-hickory forest region (Fig. 13). Only a few localities occur outside of this region in the grasslands; probably, however, these localities also are woody patches, too small to show up on the map. The boundaries of the plant associations do not coincide with the subspecies border. Most localities lie between 500 and 1500 feet elevation.

Variation. There is only limited variation, as could be expected from the small distribution of the subspecies. The shell width is statistically correlated with height, umbilicus, and whorl number, as in other taxa of *Triodopsis*. All characters show irregular geographic variation.

Triodopsis n. vulgata populations approaching *Triodopsis n. neglecta*
Plate II: 15–17

The *neglecta* populations of Alabama resemble *n. vulgata* in size and apertural features, but resemble *n. neglecta* in height and umbilicus (Table VI). These populations are considered *n. vulgata* partly because their character index falls in the range of *n. vulgata* (Alabama populations: 50–55; *n. vulgata*: 50–75; *n. neglecta*: 20–30), partly because they occur near "normal" *n. vulgata* populations, isolated from *n. neglecta* (Fig. 13). Someone might wish to treat them, however, as intergrades between *n. vulgata* and *n. neglecta*. This would also be acceptable, but the former treatment is preferable, because of the reasons mentioned. Some populations from Tennessee also resemble *n. neglecta*, although to a lesser degree than do the Alabama populations.

The origin of these populations is probably reducible to simple variation. Hybridization is unlikely, because the range of variation in these populations is hardly greater than in the assumed "pure" parental populations (Fig. 4).

The Alabama and Tennessee populations are of great significance from a taxonomic point of view. They indicate that the genetic constitution of *n. vulgata* and *n. neglecta* is so similar that interbreeding between them would occur should they be in contact with each other. It therefore seems justified to consider the two forms conspecific. A similar case was encountered in *T. j. juxtidens* and *j. discoidea*.

Summary. (1) *Triodopsis neglecta* has two subspecies: *n. neglecta* and *n. vulgata*. The former was considered by earlier workers to be a separate species, the latter a subspecies belonging to *T. fraudulenta*. *Triodopsis n. vulgata* includes *T. hopetonensis claibornensis* as a synonym.

(2) *Triodopsis n. vulgata* is distributed over a vast area; *T. n. neglecta* is a peripheral isolate.

Table VI

Range of Variation in Alabama Populations of *Triodopsis n. vulgata*. For Comparison, the Range of Variation of *n. neglecta* and of *n. vulgata*, Exclusive of the Alabama Populations, is Also Shown. Arrows Point Toward the Taxon to Which the Alabama Population Bears the Greater Similarity.

Name	Distribution	Width in mm	Height to width ratio	Umbilicus to width ratio	Upper to lower tooth ratio	Character index
T. n. neglecta	Ozarks	9.9–13.2	0.41–0.53 ↑	0.20–0.30 ↑	1.08–1.46	20–30
variant *n. vulgata*	Alabama	14.6–16.8 ↓	0.46–0.51	0.24–0.29	1.09–1.16 ↓	50–55 ↓
T. n. vulgata exclusive of Alabama populations	Ontario to Tennessee	12.2–19.8	0.41–0.63	0.16–0.30	1.00–1.29	50–75

(3) Both subspecies prefer elevations of between 500 and 1500 feet. The northern limit of distribution of *T. n. vulgata* is probably determined by the northern boundary of the beech-maple association.

(4) Both subspecies show primary intergradation and irregular geographic variation; it is surprising that with such an extensive range *n. vulgata* has developed no cline.

Triodopsis pendula Hubricht
Plate II: 24–26

Triodopsis pendula Hubricht, 1952, Nautilus 65: 82. Summit of Hanging Rock Mountain, Hanging Rock State Park, Stokes County, North Carolina. Holotype ANSP 188293, paratypes ANSP 188294.

Definition. *Triodopsis pendula* is recognized here as defined by its author. It contains those populations of the *fraudulenta* complex which have mean values of 30–45 in character index.[1] The chart used for computing character index is shown in Table IV.

Description. *Triodopsis pendula* combines shell features of *T. n. vulgata* with apertural features of *T. n. neglecta*. Shell width 10.7–13.8 mm; height 5.5–7.2 mm, height to width ratio 0.50–0.59; umbilicus 2.0–3.2 mm, umbilicus to width ratio 0.19–0.25; whorl number 4.9–5.8, whorl to width ratio 0.41–0.49; upper tooth to lower tooth ratio 1.09–1.34; embryonic whorls and sculpture as in *n. vulgata*; aperture trapezoid, dished in region of upper lip tooth; lip swelling well developed, upper lip swelling deeply receding, lower marginal; upper lip tooth moderately broad, flat, sometimes bifid, lower lip tooth normal, located near columella; parietal lamella gently bent to slightly angular, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis pendula* differs from *T. n. vulgata* in that the shell is smaller and the lower lip tooth closer to the columella (higher upper tooth to lower tooth ratio). From *T. n. neglecta* it is differentiated by its narrower umbilicus and the looser coiling of the shell; also, the last whorl behind the aperture is more than 1.5 times wider than the penultimate one in *pendula*, less than 1.5 times in *n. neglecta*. *Triodopsis pendula* may also be mistaken for *T. rugosa*. However, the aperture is dished, the lower lip tooth is closer to the columella, and the last whorl is wider in *pendula* than in *rugosa*.

Distribution. *Triodopsis pendula* occurs in three isolated areas, in North Carolina–Tennessee, in Pennsylvania, and in Ohio (Fig. 13). The Ohio record (MCZ 81499) is open to question, but may be true. The other two areas lie along the eastern and

[1] Two populations of *T. n. neglecta* also have mean values of 30. The overlap is caused by the fact that *pendula* resembles *n. neglecta* in apertural features utilized in making the character index. Notwithstanding this overlap in character index, the two forms can be safely distinguished.

northeastern periphery of the range of *n. vulgata*. This disjunct distribution pattern may indicate that the species is disappearing, or may be indicative of a hopping dispersal. Unfortunately, we have no proof either way.

The *measured material* comes from the following localities: *Pennsylvania*: Adams County (ANSP). *Ohio*: Lorain County (MCZ). *North Carolina*: Stokes (2 samples), Rowan, and Davidson counties (ANSP); Stokes and Catawba counties (JV). *Tennessee*: Carter County (ANSP). A total of 9 samples, 1–10 specimens each, 34 specimens altogether.

Ecology. *Triodopsis pendula* lives in mixed oak-pine, oak-chestnut, and beech-maple forests (Fig. 13). All localities lie between 500 and 1500 feet elevation, except the one in Tennessee, which comes from a higher altitude. At this locality, *pendula* appears to coexist with *n. vulgata*; at least the museum lot contains one specimen of *pendula* among several of *n. vulgata*.

Variation. As a consequence of the small population and limited distribution, the variation is restricted. The measured characters are statistically correlated with each other; the geographic variation is irregular.

Systematics. *Triodopsis pendula* is specifically distinct from *T. n. vulgata*, because it overlaps and apparently coexists with that form without interbreeding.

Summary. *Triodopsis pendula* is a monotypic species, with disjunct distribution, limited variation, and a small population.

Triodopsis fraudulenta (Pilsbry)
Plate II: 21–23

Polygyra tridentata var. *fraudulenta* Pilsbry, 1894, Proc. Acad. Nat. Sci. Philadelphia 46: 20, pl. 1, fig. 6. Morgan County, West Virginia, opposite Hancock, Maryland. Type ANSP 64725.

Triodopsis picea Hubricht, 1958, Trans. Kentucky Acad. Sci. 19: 73. Spruce Knob, Pendleton County, West Virginia. Holotype ANSP 202186, paratypes ANSP 202185.

Definition. *Triodopsis fraudulenta* combines the taxa formerly known as *T. f. fraudulenta* and *T. picea*; the former *f. vulgata* is excluded. A character index was not prepared for this species.

Description. Shell width 12.7–16.9 mm, height 6.7–9.0 mm, height to width ratio 0.45–0.63; umbilicus 1.9–3.9 mm, umbilicus to width ratio 0.15–0.24; number of whorls 5.2–6.1, whorl to width ratio 0.34–0.43; upper tooth to lower tooth ratio 0.96–1.22; embryonic whorls and sculpture as in *n. vulgata*; aperture oval-rectangular, lip swelling thick, lower lip swelling forming a straight edge; upper lip tooth very broad and deeply receding, located on right side of aperture; lower lip tooth narrower and marginal, located at middle of lower lip or closer to columella; parietal lamella large and nearly straight; lip teeth and parietal lamella usually overlap as one looks into the aperture; in a few specimens the lip teeth and parietal lamella do not overlap, and the upper lip tooth is less receding than usual.

Differential diagnosis. *Triodopsis fraudulenta* differs from *T. n. vulgata* in that the aperture is oval-rectangular, the lower lip swelling forms a straight ledge, the lip teeth and the parietal lamella are very large, the upper lip tooth is deeply receding, and the last whorl behind the aperture is only 1.2–1.6 times wider than the penultimate one. In *n. vulgata*, the aperture is usually square, the lower lip swelling does not form a straight ledge, the armature is weaker, the upper lip tooth is moderately receding, and the last whorl behind the aperture is 1.4–1.8 times wider than the penultimate.

Distribution. *Triodopsis fraudulenta* is found in the high mountain regions of Virginia and Maryland (Fig. 13). Its range lies on the periphery of that of *n. vulgata*, with ample overlap. Surprisingly enough, it is missing from the southern Appalachians; for explanation, see ecology, below.

The *measured material* comes from the following localities: *Maryland*: Garrett,

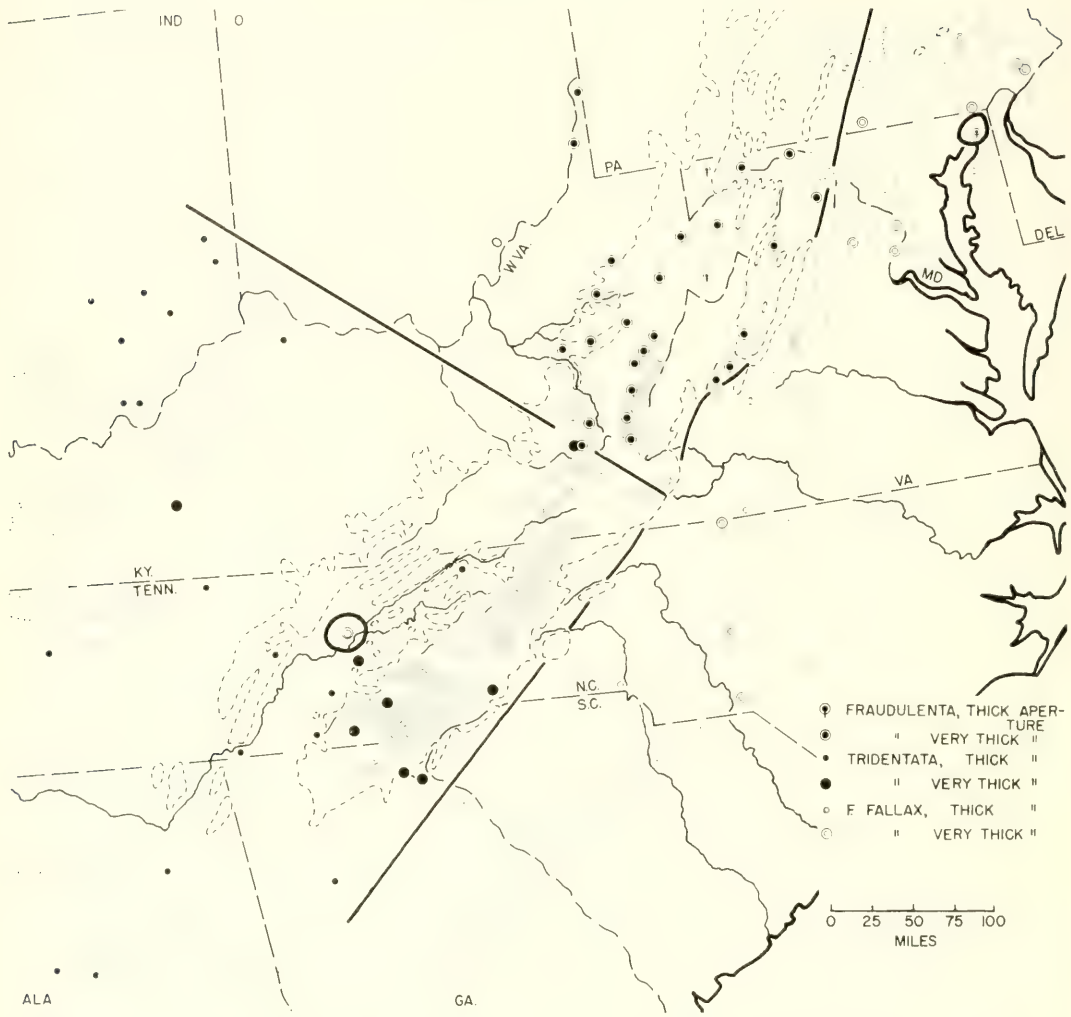


Figure 14. Distribution of *Triodopsis fraudulenta* and the mountain forms of *Triodopsis tridentata* and *Triodopsis f. fallax*. Thick, solid line separates the range of the three forms; there is almost no overlap. Other symbols refer to elevation and state boundaries, as explained in Figure 3.

Alleghany, and Cecil counties (ANSP). *Virginia*: Giles and Rockbridge counties (ANSP). *West Virginia*: Morgan (2 samples) and Pendleton counties (ANSP); Greenbrier County (MCZ). A total of 9 samples, 1–10 specimens each, 34 specimens altogether.

Ecology. *Triodopsis fraudulenta* is a mountain form of *T. n. vulgata*. It occurs between 1500 and 4000 feet, except for a few localities which lie outside these limits (Fig. 13). Thus, at Spruce Knob, Pendleton County, West Virginia, the snail reaches 4400 feet (*picea*, Hubricht, 1958), whereas in Morgan County, West Virginia, opposite Hancock, Maryland, it is found between 400 and 500 feet. It seems probable that the Potomac River and its tributaries washed the snail down to such low elevations. This mode of dispersal is observed also in *T. juxtidens*. Ironically, the lowland population had been found before

other populations of *fraudulenta* were discovered, and thus became the type population.

The area occupied by *fraudulenta* is covered by mixed mesophytic and oak-chestnut forests, except for the higher peaks, which may reach up into the evergreen zone (Fig. 13). The distribution of the forest types and the snail are not correlated.

Triodopsis fraudulenta occurs only in the higher regions of the northern Appalachians. The comparable habitats in the southern Appalchians are occupied by the mountain-form, grade D, of the related species, *T. tridentata* (Fig. 14). It seems clear that the two forms exclude one another. Each form "fills" its habitat completely, thus leaving no room for the other.

Variation. Aperture: In the populations from Spruce Knob, Pendleton County, West Virginia, and Jennings, Garrett County, Maryland, the upper lip tooth is narrower and less receding than normal for *fraudulenta*, thus approaching *T. n. vulgata*. This may be caused by introgression from *n. vulgata*, but may be due to simple variation. A definite conclusion cannot be reached, because only two populations—six specimens—are available, not enough for statistical analysis. The Spruce Knob population has been described by Hubricht as *T. picea*.

The strong development of the lip swelling, lip teeth, and parietal lamella occurs in all species of the subgenus which inhabit higher mountains, *tridentata*, *rugosa*, *fraudulenta*, and *f. fallax*. These features appear to be adaptive, but their exact significance is unknown.

Measured characters: Shell width, height, umbilicus, and whorl number are correlated statistically. Their geographic variation is irregular.

Systematics. Triodopsis fraudulenta appears to be a specialized mountain form of *T. n. vulgata*. Thus it would seem logical to consider it conspecific with the latter, as earlier workers have indeed done. But the two forms seem to have reached reproductive isolation—they do not interbreed despite a wide overlap. For this reason, it is necessary to separate them on the species level. It may be added that partial ecological isolation also has been achieved, since *fraudulenta* prefers higher areas than does *n. vulgata*.

Triodopsis picea has a somewhat narrower umbilicus, and a narrower and less receding upper lip tooth than "normal" *fraudulenta* (Hubricht, 1958). Its author also claims that it is "unique in having papillae over the upper surface of the shell." On this basis, he ranks it as a full species. I believe this to be unwarranted. The measurements of *picea* are clearly within the range of *fraudulenta* (Table VII). The upper surface of the shell of *fraudulenta*, as well as of some other species of *Triodopsis*, is papillated. Only the differences in the aperture remain. When one considers, however, how much the aperture varies in *Triodopsis*, not much importance can be attributed to these relatively minor differences. The conclusion is thus that *picea* should not be separated from *fraudulenta* on a morphological basis. The same is true of distribution. Hubricht reported *picea* from Spruce Knob, Pendleton County, Three Forks of William River, Webster County, and Rainelle, Fayette County, all in West Virginia. A population from Jennings, Garrett County, Maryland, can also be included with the above. All these localities are isolated from one another, and lie within the range of *fraudulenta*. At no locality do *picea* and *fraudulenta* occur together.

Summary. (1) *Triodopsis fraudulenta* is a monotypic species, with *T. picea* as a synonym. The former *T. f. vulgata* is excluded from the species.

(2) *Triodopsis fraudulenta* is a specialized mountain form of *T. n. vulgata*. It occurs in the northern Appalachians, primarily at higher elevations. Similar regions in the southern Appalachians are occupied by the mountain form of the related spe-

Table VII

Measurements of *Triodopsis picea* and Two Populations of *T. fraudulenta*. The Former is Considered Synonymous with the Latter.

Name	Locality	Number of specimens	Mean of: Width in mm	Height to width ratio	Umbilicus to width ratio	Whorl to width ratio	Upper to lower tooth ratio
picea types	W. Virginia	3	14.0	0.56	0.17	0.39	1.07
fraudulenta	Maryland	3	15.2	0.55	0.17	0.35	1.09
fraudulenta types	W. Virginia	1	15.7	0.54	0.20	0.36	1.18

cies, *T. tridentata*. Thus the two mountain forms show ecological exclusion.

Evolutionary relationships within the fraudulenta complex. As the morphological and distributional evidence indicates, *T. n. vulgata* may be the central stock from which developed the other members of the complex, *n. neglecta*, *pendula*, and *fraudulenta*. This form is in intimate relationship with the others, and occupies a geographically central position as well. The other forms can be derived from *n. vulgata*, and occupy positions peripheral to *n. vulgata*. It thus seems likely that they once were part of the population of *n. vulgata*, but became isolated and diverged.

The *fallax* Complex

Definition. This complex contains two polytypic species with five subspecies: *T. fallax*, with subspecies *f. fallax*, *f. obsoleta*, and *f. alabamensis*; and *T. copei*, with subspecies *c. copei* and *c. cragini*; and one, somewhat isolated monotypic species, *T. soelneri*.

Triodopsis fallax (Say)
Triodopsis fallax fallax (Say)

Plate III: 4, 5, 10, 11

Helix fallax Say, 1825, J. Acad. Nat. Sci. Philadelphia 5: 119. Neotype selected by Pilsbry (1940: 809, fig. 480a). Manayunk, Montgomery County, Pennsylvania. Neotype ANSP 25821.

Helix introferens Bland, 1860, Ann. Lyc. Nat. Hist. New York 7: 117, pl. IV, figs. 3–4. Gaston County and Salem, Forsyth County, both North Carolina. Type not seen.

Triodopsis introferens var. *minor* Tryon, 1867, Amer. J. Conch. 3: 51. ". . . the whole country east of the Rocky Mountains." Type not seen.

Definition. Triodopsis f. fallax corresponds to *T. fallax* of Pilsbry (1940). It contains those populations of the species which have mean values of 50–100 in character index A, and of 70–90 in character index B. The chart used for computing character index is shown in Table VIII.

Description. Shell width 10.1–15.5 mm; height 5.9–9.1 mm, height to width ratio 0.50–0.66; umbilicus 1.3–3.2 mm, umbilicus to width ratio, 0.12–0.22; number of whorls 5.0–6.4, whorl to width ratio, 0.38–0.56; embryonic whorls 1.4–1.5, with faint striation or almost smooth; subsequent whorls with more pronounced striae, last whorl with 3–5 strong striae per millimeter; intervals between striae smooth, papillae occurring only in umbilical region and behind aperture; aperture oval to auriculate, lip swelling thick, slightly receded, and therefore edge of aperture sharp; lip teeth large, upper lip tooth moderately to deeply receding, lower lip tooth marginal; a small or large fulcrum present inside last whorl; usually a small, flat projection present on face of lower lip.

Differential diagnosis. Triodopsis f. fallax is easily distinguished from *T. fraudulenta* because it has a fulcrum and a narrow umbilicus which expands suddenly at the last whorl. *T. fraudulenta* has no fulcrum, and its umbilicus is wide at the beginning, expanding moderately at the last whorl.

TABLE VIII

CHART FOR COMPUTING CHARACTER INDEX FOR *TRIODOPSIS FALLAX*.

Character Index A

SCORE	APERTURE GRADE	FULCRUM	
0	A	none	*f. obsoleta*
20	B	small	↑
40	C	large	↓
60	D	—	*f. fallax*

Method of calculation: A specimen having an aperture grade D and a large fulcrum is scored 60 + 40 = 100, the maximum possible score.

Character Index B

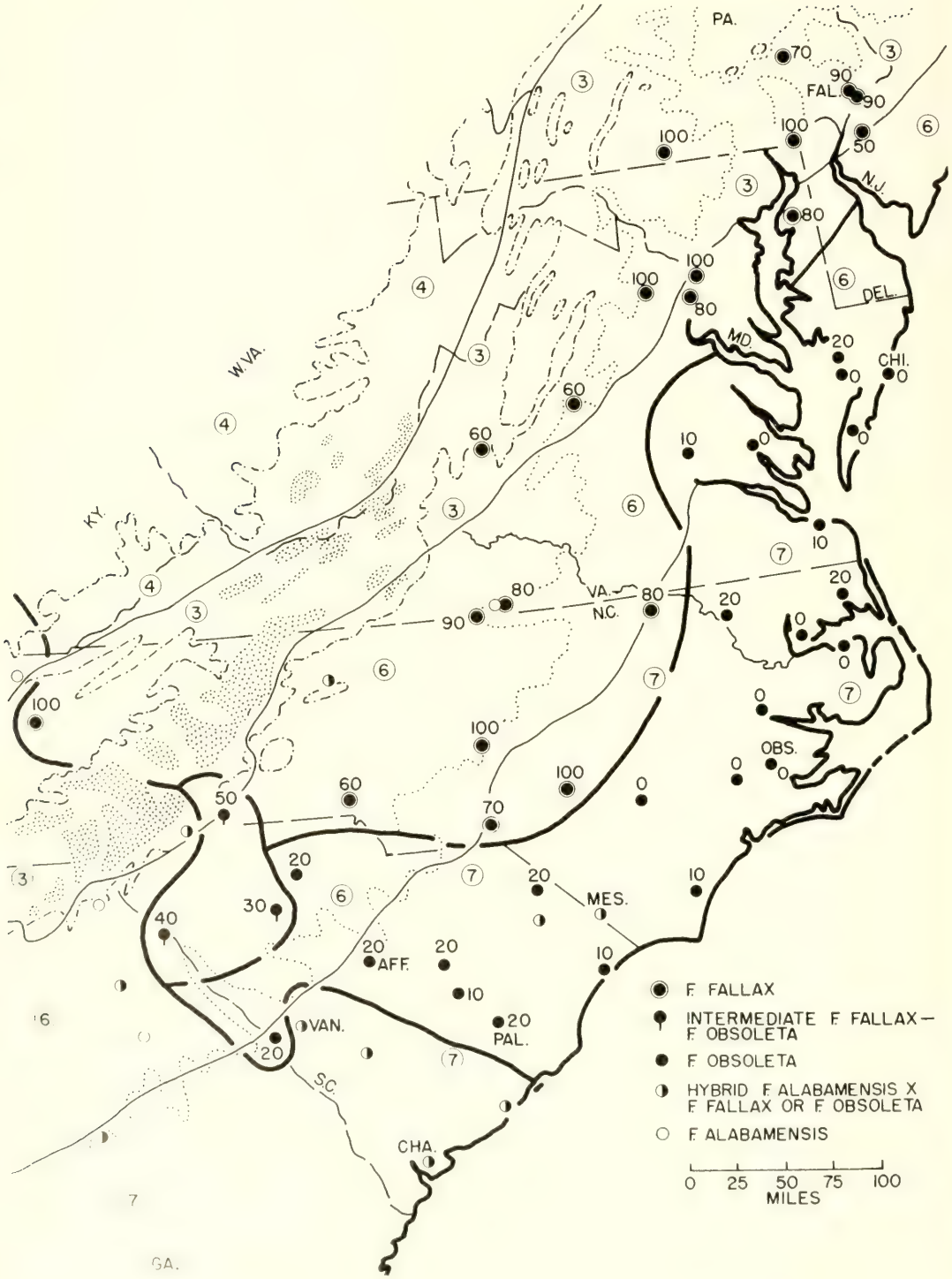
SCORE	WHORL TO WIDTH RATIO	ANGLE OF RIGHT SIDE OF APERTURE (IN DEGREES)	PARIETAL LAMELLA	EDGE OF APERTURE	
0	0.67–0.68	77.5–80.0	arcuate	swollen	
5	0.66	82.5–85.0			*f. alabamensis*
10	0.64–0.65	87.5			↑
15	0.63	90.0–92.5	slightly angular	slightly swollen	
20	0.61–0.62	95.0			
25	0.60	97.5–100.0			
30	0.58–0.59	102.5	sharply angular, straight, missing	sharp	
35	0.57	105.0–107.5			
40	0.55–0.56	110.0–112.5			
45	0.54				
50	0.53				
55	0.52				
60	0.50–0.51				
65	0.49				
70	0.47–0.48				
75	0.46				
80	0.44–0.45				
85	0.43				
90	0.41–0.42				
95	0.40				*f. fallax-*
100	0.38–0.39				*f. obsoleta*

Method of calculation: a specimen with a whorl to width ratio of 0.38, an aperture angle of 112.5 degrees, a sharply angular parietal lamella, and a sharp aperture edge is scored (100 + 40 + 30 + 30)/2 = 100, the maximum available score.

Distribution. Triodopsis f. fallax ranges from New Jersey to North Carolina. Westward, it reaches to the Blue Ridge Mountains, and in one place to Tennessee (Fig. 15). It overlaps *T. tridentata* slightly, *T. j. juxtidens* extensively.

The *measured material* comes from the following localities: *New Jersey*: Gloucester County (ANSP). *Pennsylvania*: Philadelphia, Montgomery, Berks, Chester, and Adams counties (ANSP). *Maryland*: Kent County (ANSP). *Virginia*: Alex, Fairfax, Prince William, Albermarle, Rockbridge, and Pittsylvania counties (ANSP). *North Carolina*: Rockingham, Gaston, Randolph, Richmond, Cumberland, and Warren counties (ANSP). *Tennessee*: Knox County (MCZ). A total of 20 samples, 2–30 specimens each, 187 specimens altogether.

Ecology. Triodopsis f. fallax inhabits mixed oak-pine and oak-chestnut forests (Fig. 15). It reaches from about 300 feet on the coastal plain to about 1500 feet in the Blue Ridge Mountains. It is probable that elevation, or factors associated with el-


PA.
70
90
FAL.
90
100
100
50
N.J.
80
DEL.
100
100
80
MD.
20
CHI.
0
60
60
10
0
0
W.VA.
KY.
10
VA.
80
80
N.C.
90
20
10
0
0
100
100
0
OBS.
0
0
100
60
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70
20
20
MES.
10
40
30
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AFF.
20
10
10
20
PAL.
VAN.
20
SC.
CHA.
GA.
F. FALLAX
INTERMEDIATE F. FALLAX—F. OBSOLETA
F. OBSOLETA
HYBRID F. ALABAMENSIS X F. FALLAX OR F. OBSOLETA
F. ALABAMENSIS
0 25 50 75 100
MILES

evation, determines the subspecies border to a great degree. The forest boundaries do not have such a role.

It remains obscure to me why *T. f. fallax* fails to reach above 1500 feet in the Blue Ridge Mountains. Judged by its heavy armature, *f. fallax* is a "mountain-adapted" snail (p. 239), and we would thus expect to find it at high altitudes. Competition and exclusion are in all likelihood not responsible for its absence, since no other mountain-adapted species of *Triodopsis* occurs in the region. Perhaps we should not consider the heavy armature an adaptation to the mountains; in most other cases, however, this feature is certainly associated with mountainous habitats, and in the species *fallax*, the heavy armature is restricted to the subspecies which lives in the highest regions of the species range.

In my experience, *T. f. fallax* does not coexist with *T. f. juxtidens*, although they extensively overlap and both inhabit woods. The size of these animals is approximately the same, and so are their ecological requirements; both live in the litter layer and feed on decaying plant material and fungi. Hence there is competition and resulting habitat exclusion between them. The similarity in the ecological requirements is striking, if we consider the wide differences in morphology. The morphological and ecological differences have evidently evolved at very different rates. *Triodopsis f. fallax* also shows exclusion with *T. tridentata*, which it narrowly overlaps.

Systematics. The first description of the taxon *fallax* was given by Say in 1825. Mistakenly, however, his name was applied to another taxon, today known as *fraudulenta*, whereas the true *fallax* was called *introferens*, Bland, 1865. Tryon pointed out this error in 1867. Subsequently, *fraudulenta* was changed to *fallax*, *introferens* became synonymous with the latter, and the name *fraudulenta* was transferred to the proper taxon.

Triodopsis fallax intergrades and probably hybridizes with *T. obsoleta* and *T. v. alabamensis* (p. 195, names in old usage). For this reason, I consider it conspecific with these forms. Since *fallax* is the oldest of the three names, the proper name of this species is *T. fallax*, and the earlier *fallax* becomes the nominal subspecies of this species.

Triodopsis fallax obsoleta (Pilsbry) Plate III: 1–3, 6, 7

Polygyra fallax obsoleta Pilsbry, 1894, Nautilus 7: 140. Newbern, Craven County, North Carolina. Type ANSP 57195.

Triodopsis hopetonensis subsp. *chincoteagensis* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 813, fig. 480d. Chincoteague Island, Accomac County, Virginia. Type ANSP 151482.

Triodopsis fallax subsp. *affinis* Hubricht, 1954, Nautilus 68: 28. Columbia, Richland County, South Carolina. Paratype ANSP 190820.

Triodopsis palustris Hubricht, 1958, Trans. Kentucky Acad. Sci. 19: 74. Flood-plain of Santee River, 5.5 miles southwest of St. Stephens, Berkeley County, South Carolina. Holotype ANSP 202187 and paratypes ANSP 202188.

Definition. Triodopsis f. obsoleta combines *fallax obsoleta* or *hopetonensis obsoleta*, *h. chincoteagensis*, *f. affinis*, and *palustris* of earlier authors. It contains those populations of the species which have

←

Figure 15. Distribution and the geographic variation of character index A of *Triodopsis f. fallax*, *f. obsoleta*, and intermediates between the two subspecies. Solid, thick line separates the ranges of the three groups. AFF, type locality of *affinis*; CHI, *chincoteagensis*; OBS, *f. obsoleta*; PAL, *palustris* (these four forms are all combined in *f. obsoleta*). FAL, *f. fallax*. CHA, *charlestonensis*; MES, *messana*; VAN, *vannostrandi* (these three forms are considered hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta*, or intermediate between *f. fallax* and *f. obsoleta*). Numbers without a circle are mean values of samples in character index A; samples of *f. obsoleta* range from 0 to 20, intermediate between *f. obsoleta* and *f. fallax*, 30–50, *f. fallax*, 50–100. Note that *f. fallax* and *f. obsoleta* are sharply separated in the northern and middle parts of the range, intergrading in the south. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

mean values of 0–20 in character index A and 70–90 in character index B. The chart used for computing character index is shown in Table VIII (p. 185).

Description. Shell width 9.7–13.5 mm; height 5.1–8.8 mm, height to width ratio 0.47–0.65; umbilicus 1.2–2.7 mm, umbilicus to width ratio 0.11–0.22; number of whorls 4.5–6.0, whorl to width ratio 0.39–0.53; embryonic whorls 1.4–1.5, with faint striation or almost smooth; subsequent whorls with more pronounced striae, last whorl with 3–5 striae per millimeter; space between striae smooth, except in umbilical region and behind aperture, where covered with papillae; aperture auriculate, sometimes oval; lip swelling thin to moderately thick and slightly receded, thus edge of aperture sharp; lip teeth lacking, small, or medium sized, upper lip tooth at most moderately receded, lower lip tooth marginal; parietal lamella small and straight or moderately large and angular; fulcrum usually absent; flat projection on face of lower lip absent or very small.

Differential diagnosis. Triodopsis f. obsoleta differs from *f. fallax* in that the aperture is more auriculate, the lip teeth and parietal lamella smaller, the fulcrum smaller or absent. Also, it usually has relatively fewer whorls than *f. fallax.*

Distribution. Triodopsis f. obsoleta is distributed along the eastern seaboard from Delaware to Georgia. On the west it is adjacent to *f. fallax.* The two forms are sharply separated in the northern and middle regions, but intergrade in the southern region (Fig. 15).

The *measured material* comes from the following localities: *Maryland*: Somerset County (2 samples, ANSP). *Virginia*: Accomac, Northampton, Henrico, King William, and Norfolk counties (ANSP). *North Carolina*: Sampson, Camden, Chowan, Tyrell, Beaufort, Craven, Jones, Hanover, and Northampton counties (ANSP). *South Carolina*: Dillon, Horry, Sumter, Clarendon, Richland, Union, and Berkeley counties (ANSP). *Georgia*: Richmond County (MCZ). A total of 24 samples, 2–31 specimens each, 434 specimens altogether.

Ecology. Triodopsis f. obsoleta occurs in the lower regions of the southeastern coastal plain, up to about 300–400 feet, rarely to 500 feet (Fig. 15). Since the subspecies border runs predominantly parallel to the contour lines, elevation, or factors associated with it, seems to determine the distributional limits of the snail. The area is covered by mixed oak-pine and southeastern evergreen forests (Fig. 15). Both kinds of forests seem to be equally suitable habitats for the snail. Several records are known from offshore islands.

Triodopsis f. obsoleta shows habitat exclusion with *T. j. juxtidens.*

Systematics. The taxon *obsoleta* was originally assigned by its author as a subspecies to *Triodopsis fallax.* A few years later, however, he transferred it to *T. hopetonensis*, and this is how it became commonly known. The change was for the worse, however, since *hopetonensis* is not a valid name, the type population being a hybrid between *f. alabamensis* and *f. fallax* or *f. obsoleta.* Also, *obsoleta* and *fallax* intergrade (see p. 189), and therefore should remain in the same species. I propose, in consequence, to reinstate the original name, although not quite with the original content.

In contrast to the views set forth in this paper, Hubricht (1953: 120) and Grimm (*in litt.*) consider *T. obsoleta* and *T. hopetonensis* as two separate species. Their *T. obsoleta* is what I consider grade A (see below) of *T. f. obsoleta*, and their *T. hopetonensis* corresponds largely to my grade B of *T. f. obsoleta.* Hubricht argues that there are differences between these grades in aperture, size, height, umbilicus, and color. Grimm speaks of differences in height of the spire and luster of the shell. On the basis of extensive measurements and studies, I cannot confirm that any of these differences is diagnostic (Fig. 16, and Table IX). The two grades cannot be separated on distributional grounds either, because

their areas overlap, and they frequently occur together in the same population. I feel it is justified, therefore, to combine these grades into the single taxon, *T. f. obsoleta.*

Hubricht (1953: 121) also stated that ". . . in December, a series of specimens of *T. obsoleta* from two localities and specimens of *T. hopetonensis* from two other localities were examined anatomically. In all the specimens of *T. obsoleta*, the penis was fully developed, but in the specimens of *T. hopetonensis* all had the penis very small and immature in appearance. This suggests that a factor in the reproductive isolation of these two species may be a difference in the breeding season." This conclusion seems to be at variance with Grimm's experiments (*in litt.*). The latter investigator repeatedly crossed *hopetonensis* and *obsoleta* in the laboratory, which, of course, he could not have done if the two forms had different breeding seasons.

Three forms, known as *T. hopetonensis chincoteagensis*, *T. fallax affinis*, and *T. palustris*, appear to belong to *f. obsoleta.* The detailed argument for this assignation is as follows.

Triodopsis h. chincoteagensis is supposedly characterized by its small size, narrow umbilicus, and reduced lip teeth. These features occur, however, in many *T. f. obsoleta* populations, and thus the morphological separation does not hold (Table IX). The form in question occurs on an offshore island in Virginia (Fig. 15), "isolated" from the mainland population. This fact might seem to justify its subspecific rank, but the failure of the population to achieve any appreciable morphological divergence seems to indicate that the isolation is incomplete or of very brief standing. And for these reasons, a subspecific separation of the population is unfounded.

Triodopsis palustris has a larger and flatter shell, and a wider umbilicus than do most specimens of *T. f. obsoleta*, although there is no gap between them (Table IX). Rather, *palustris* represents the extremes of the variation of *f. obsoleta.* This form has been reported from the flood plains of the Savannah and Santee rivers and from the Altamaha Swamp (Hubricht, 1958). It thus appears to be a feebly characterized polytopic form, which, I believe, should not be recognized taxonomically.

Triodopsis f. affinis, from South Carolina, differs from *T. f. obsoleta* in that some specimens (4 of 11) have a swollen peristome. Since the latter feature normally occurs in *T. f. alabamensis, affinis* appears to be hybrid between *f. obsoleta* and *f. alabamensis.* The contribution of the *f. alabamensis* genes is so small, however, that the mean value of the population in character index B, 70, is still within the range of *f. obsoleta*, 70–90; *T. f. alabamensis* has mean values of 20–40, hybrids, 45–65. For this reason, I consider *f. affinis* synonymous with *f. obsoleta*, and not a hybrid.

Hubricht, who described *f. affinis*, also changed his opinion on its status. In a recent letter he wrote: "*T. f. affinis* is a hybrid swarm between *T. fallax* and *T. alabamensis.*" It seems to me more likely that *f. obsoleta* is the first parent, because it occurs next to the area of *affinis*, whereas *f. fallax* does not. Furthermore, *T. f. fallax* and *f. obsoleta* intergrade in South Carolina, the region in question, and thus it may well be that intergrades, rather than "pure" *f. obsoleta* or *f. fallax*, produced *f. affinis* by interbreeding with *f. alabamensis.* But the difference is really not important.

Populations intermediate between *Triodopsis f. fallax* and *f. obsoleta*

A few samples of *T. fallax* are intermediate between *f. fallax* and *f. obsoleta* in morphological characters. This is expressed by the mean values of these populations in character index A, which vary from 30 to 50; those of *f. fallax* are 50–100, of *f. obsoleta*, 0–20. These samples are also intermediate in their geographic position (Fig. 15).

TABLE IX

MEASUREMENTS OF REPRESENTATIVE POPULATIONS OF *TRIODOPSIS HOPETONENSIS CHINCOTEAGENSIS*, *T. H. OBSOLETA*, *T. F. AFFINIS*, AND *T. PALUSTRIS*. ALL THESE TAXA BELONG TO *F. OBSOLETA*. *TRIODOPSIS F. AFFINIS* SHOWS SOME RESEMBLANCE TO *T. F. ALABAMENSIS* IN APERTURAL FEATURES.

NAME	LOCALITY	GRADE		NO. OF SPECIMENS	MEAN OF			CHARACTER INDEX	
		APERTURE	FULCRUM		WIDTH IN MM	HEIGHT TO WIDTH RATIO	UMBILICUS TO WIDTH RATIO	A	B
identified as *obsoleta*, but comes from type locality of *chincoteagensis*	Chincoteague Island, Accomac County, Virginia	A	–	30	10.8	0.55	0.14	0	85
obsoleta	Criesfield, Somerset County, Maryland	A	–	17	11.1	0.55	0.13	0	85
types of *obsoleta*	Newbern, Craven County, North Carolina	A, B	–	5	11.7	0.53	0.17	0	85
obsoleta	Chocowinity, Beaufort County, North Carolina	A, B	–	25	12.4	0.52	0.18	0	90
paratypes of *f. affinis*	Columbia, Richland County, South Carolina	B	–	11	11.4	0.56	0.16	20	70
types of *palustris*	St. Stephens, Berkeley County, South Carolina	B	–	3	13.7	0.50	0.19	20	80

These populations may either represent primary intergradation between *T. f. fallax* and *f. obsoleta*, or be hybrids between the two subspecies. The fact that the range of their variation is not significantly larger than that of samples from either "pure" subspecies indicates that the former assumption is true. The fact, however, that intermediate populations occur only in the south, whereas in the north *f. fallax* and *f. obsoleta* are sharply separated from one another, indicates hybridization (see p. 192). Because the amount of material at hand is rather small, the question cannot be finally settled.

Measured samples of the intermediate populations come from the following localities: *North Carolina*: Polk County (ANSP). *South Carolina*: Laurens County (ANSP). *Georgia*: Hart County (ANSP). A total of 3 samples, 2–13 specimens each, 26 specimens altogether.

These intermediate populations are significant in that they demonstrate the conspecificity of *f. fallax* and *f. obsoleta*.

The variation of Triodopsis f. fallax, f. obsoleta, and intermediates between them. Since the variation of *T. f. obsoleta* is in several respects a natural continuation of that of *f. fallax*, it is reasonable to discuss the variation of the two subspecies together.

Individual characters. Aperture: According to the development of the aperture, four phases can be distinguished, referred to as aperture grades A, B, C, and D (Plate III). In grade A, the lip swelling is thin, the lip teeth and parietal lamella are absent or small; the upper lip tooth, when present, is slightly receding; the parietal

lamella, when present, is short and straight. In grade B, the lip swelling is moderately thick, the lip teeth moderately large, the upper one slightly receding; the parietal lamella is also moderately large, and usually broken at a sharp angle; the lip teeth and parietal lamella do not obstruct the aperture. In grade C, the lip swelling is thick, the lip teeth are large, the upper one wide and receding; the parietal lamella is large and angular; these structures obstruct the aperture considerably. In grade D, the lip swelling is very thick, the lip teeth very large, the upper lip tooth very wide and deeply receding; the parietal lamella is also very large and angular; the lip teeth and parietal lamella seem to touch or even overlap one another when one looks into the aperture. The variation of the aperture grades is continuous. Thus the numbers and limits of the grades are, to some extent, arbitrary; a different number of grades might be recognized by other investigators.

Specimens of grades A + B, and C + D commonly occur together in the same population, but grade B specimens also may be found occasionally in C + D populations, or C in A + B. Populations consisting of A, B, or A + B specimens form subspecies *f. obsoleta*; those consisting of C, D or C + D specimens, *f. fallax*; populations consisting of B + C specimens constitute the intermediates. It might be noted that grade B specimens have been identified as *hopetonensis*, and grade A specimens as *obsoleta*, by most workers in the field.

Grade A specimens occur in a wide zone along the seashore; grade B specimens in a somewhat higher zone, and grades C and D still higher. These zones, however, overlap widely. The geographic distribution of the four aperture grades thus reflects an underlying, gradual, change in the environment, primarily in elevation. This conclusion is taxonomically important, since it cautions against attributing diagnostic importance to minor variations in the aperture.

Fulcrum: According to the degree of development, three types can be distinguished: fulcrum absent, small, or large. The three types intergrade. Specimens without a fulcrum usually belong to aperture grades A or B, occasionally to C or D. A small fulcrum is common in grades C and D, rare in B. A large fulcrum is common in grades D and C, less common in B. Thus, the development of the armature and the fulcrum is correlated to some extent. Populations of specimens without a fulcrum form *f. obsoleta*; those composed of specimens with a small or large fulcrum are *f. fallax*; populations which combine specimens with a small fulcrum or without one are the intermediates.

Specimens without a fulcrum usually occur near the seashore, those with a large fulcrum in the higher regions. So far, the arrangement is roughly zonal. Specimens with a small fulcrum do not, however, occur zonally; instead, they are found in three isolated groups in the northern, middle, and southern parts of the range. Thus the geographic variation of the fulcrum is not quite concordant with that of the aperture.

Parietal lamella: This may be (1) small and straight, (2) sharply angular, (3) slightly angular, or (4) arcuate (Plate III). The small and straight lamella is actually a reduced form of the sharply angular type, of which only the distal portion remains. This type is characteristic of specimens of aperture grade A, in which the lip teeth are reduced as well. Among the three remaining types, the sharply angular parietal lamella is the most common; it prevails in all aperture grades except A. The slightly angular and arcuate types are common only in a few southern populations. This is possibly caused by gene flow from the southern subspecies, *f. alabamensis*, in which the arcuate type is dominant. The slightly angular types in these cases may be the product of the mixing of the sharply angular and arcuate types.

The small, straight, type occurs in areas

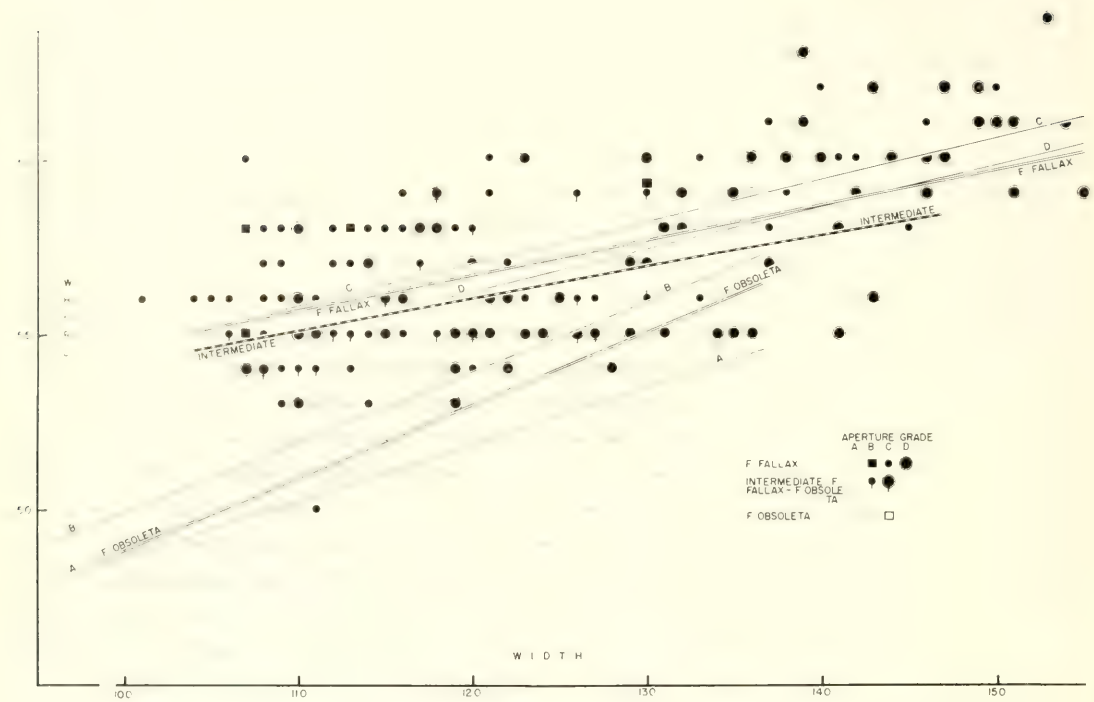


Figure 16. Scatter diagram of whorl number versus shell width in the four aperture grades of *Triodopsis f. fallax, f. obsoleta,* and intermediates between the two subspecies. The regression lines of whorl number on width show that aperture grade A is very close to B, and C to D, whereas B and C are farther apart. Scale of width in millimeters.

near the seashore; the sharply angular type prevails elsewhere, except for a few spots in the south where the slightly angular and arcuate types are also common.

Measured characters. The shell width is correlated with height, umbilicus, and whorl number. The regression lines of whorl number to width, calculated separately for the four aperture grades (Fig. 16), indicate closer relationships between grades A and B, and C and D, than between B and C. This is important from a taxonomic standpoint (p. 193).

The geographic variation of the measured characters is irregular. As an example, the variation of the whorl to width ratio is illustrated (Fig. 19, p. 197).

Character index: In the analysis of *T. f. fallax* and *f. obsoleta*, character index A is used. This is based upon a combination of the aperture and fulcrum grades (Table VIII, p. 185). It would, of course, have been better to use more than two characters. This could not be done, however, because the other characters overlap so widely that they would only confuse the situation, rather than clarify it.

The mean values of populations in character index A vary from 0 to 100. Populations with low mean values (*f. obsoleta*) are found near the Atlantic sea coast, those with high values (*f. fallax*) farther inland (Fig. 15). The transition from low to high mean values is gradual in the southern part of the range, but extremely sharp in the middle and northern parts.

This pattern might be what Huxley refers to as "widening of the hybrid belt" (1942: 250). According to this hypothesis, *f. fallax* and *f. obsoleta* were isolated from each other in an earlier period; recently, however, they re-established contact and started to hybridize. The hybrids are inferior to the parents; they are therefore se-

lected against. Since the hybridization presumably started in the northern part of the range earlier than in the southern, the hybrids have been completely eliminated from the north, but still remain in the south. The absence of the hybrids makes the transition in character index sharp, their presence makes it gradual.

This theory sounds appealing, but it remains mere speculation until we can prove that the intergrading populations of the south are really hybrids, and that the hybrids are of inferior viability. Unfortunately, the available material is too limited for statistical analysis, and no experiments have been done on the viability of the hybrids. Other possible explanations also suffer from lack of evidence; thus there is, at present, no satisfactory explanation of the above phenomenon.

The geographic variation of character index A provides the foundation upon which the classification put forth in this paper rests (Fig. 15). It is argued here that only two taxa should be separated in the *fallax-obsoleta* group (excluding *f. alabamensis*), and the separation should be on the subspecies level. The geographic variation of character index A shows two groups of populations, one with low and another with high mean values, and it also shows that the two groups intergrade in the south. Other evidence comes from a study of the aperture, and of some metric characters, such as whorl number and width (Fig. 16), which also show the existence of two subspecies, one combining aperture grades A and B, the other, C and D.

The finding that *f. fallax* and *f. obsoleta* behave as subspecies in certain areas of the range, and as distinct species in others, is of great theoretical interest, since it shows that isolating mechanisms between two populations can develop at different rates in different parts of the range. The populations involved are actually neither species nor subspecies, but intermediate.

Triodopsis fallax alabamensis (Pilsbry)
Plate III: 9, 14, 15

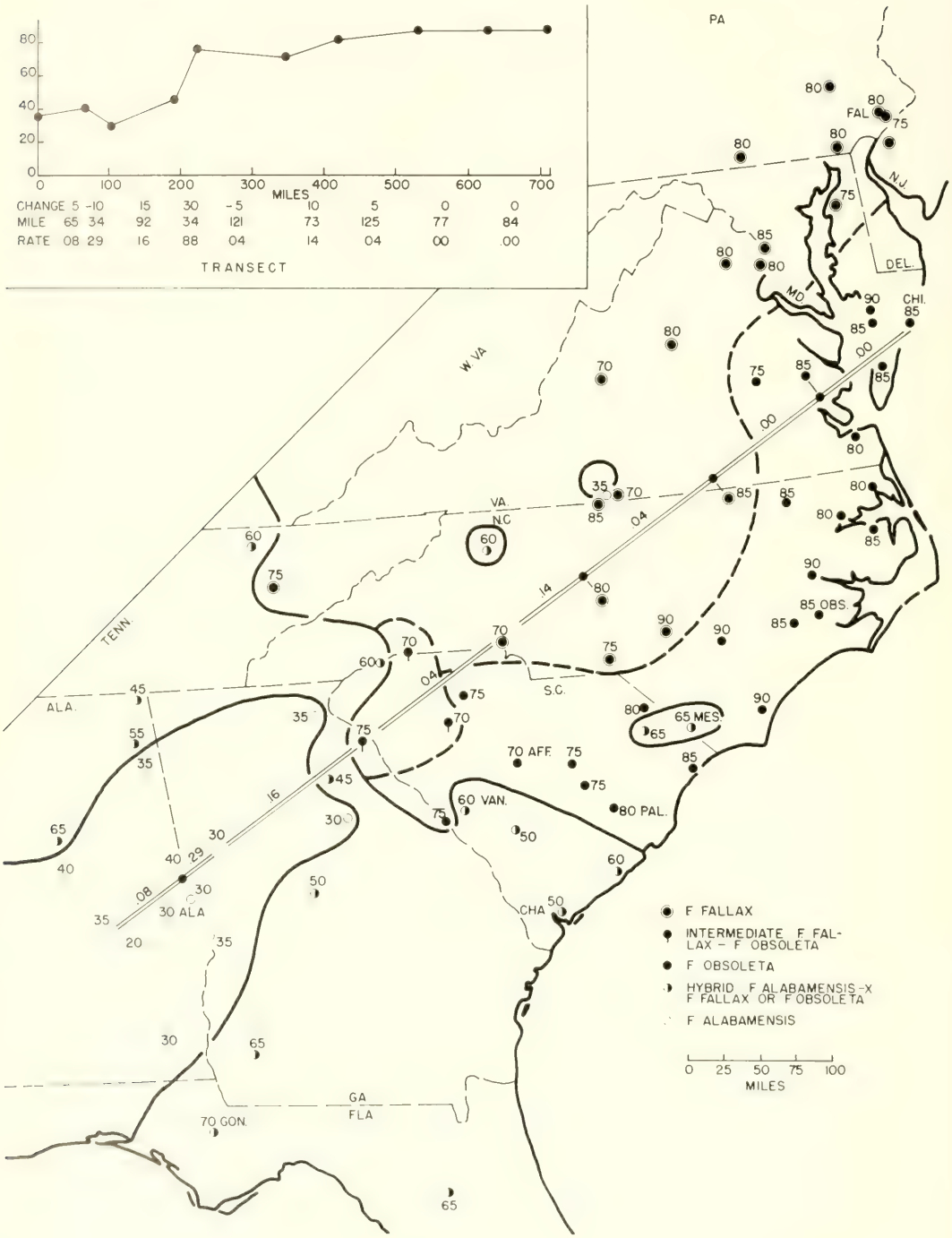
Polygyra alabamensis Pilsbry, 1902, Nautilus 16: 30. Elamville, Barbour County, Alabama.

Definition. *Triodopsis f. alabamensis* corresponds to *T. vannostrandi alabamensis* of earlier authors. It contains those populations of the species which have mean values of 20–40 in character index B. The chart used in computing character index B is shown in Table VIII (p. 185).

Description. Shell width 8.6–13.1 mm; height 4.9–7.5 mm, height to width ratio 0.48–0.66; umbilicus 1.2–3.0 mm, umbilicus to width ratio 0.12–0.24; number of whorls 5.1–7.0, whorl to width ratio 0.49–0.68; embryonic whorls 1.4–1.5, nearly smooth to finely striated; subsequent whorls with increasingly stronger striae; last whorl with 3–4 strong striae per millimeter; aperture square to trapezoid, slightly depressed; lip swelling medium thick, marginal, thus edge of aperture swollen; lip teeth medium large, upper lip tooth slightly receding; lower lip tooth marginal; parietal lamella arcuate or slightly or sharply angular; no projection on face of lower lip swelling.

Differential diagnosis. *Triodopsis f. alabamensis* is distinguished from *f. fallax* and *f. obsoleta* by its tighter coiling, square aperture, and swollen peristome. The latter two subspecies have looser coiling, an auriculate aperture, and a sharp peristome. From *T. c. cragini*, another similar form, it is separated by its greater number of whorls, and its smaller and less broad upper lip tooth.

Distribution. *Triodopsis f. alabamensis* occurs in eastern Alabama and northern Georgia (Fig. 17). It is also known from Danville, Pittsylvania County, Virginia, collected by Hubricht (misidentified as *T. f. affinis*). There is a sample of *f. alabamensis* in the collection of the ANSP from Jackson County, Texas, identified as *T. cragini* (ANSP 186723, collected by Cheatum). If my identification is correct, this locality is erroneous. Only *T. c. copei* and *T. c. cragini* occur in Texas.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70 AFF.
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INTERMEDIATE F FALLAX – F OBSOLETA
F OBSOLETA
HYBRID F ALABAMENSIS-X F FALLAX OR F OBSOLETA
F ALABAMENSIS
0 25 50 75 100
MILES

The *measured material* comes from the following localities: *Virginia*: Pittsylvania County (ANSP). *Georgia*: Habersham, Greene, Coweta, and Muscogee counties (MCZ). *Alabama*: Randolph, Chambers, Lee (2 samples), Elmore, and Shelby counties (ANSP); Cherokee, Lee, Macon, and Dale counties (MCZ). A total of 15 samples, 2–27 specimens each, 144 specimens altogether.

Ecology. *Triodopsis f. alabamensis* occurs in mixed oak-pine and southeastern evergreen forests. In elevation, it ranges from a few hundred to about 1500 feet. Neither the plant associations nor the elevation play a major role in determining the distributional borders of the subspecies, except in the northwest, where the subspecies border closely follows the boundaries of the mixed oak-pine forests.

Variation. The *aperture* shows moderate variation. The lip teeth of most specimens correspond in size to those of aperture grade B of the *f. fallax-f. obsoleta* group. Occasional specimens with smaller lip teeth also occur. The *fulcrum* is absent, except in a single specimen from Auburn, Lee County, Alabama, which, incidentally, is the type locality of the subspecies. The occurrence of a specimen with a fulcrum at this locality is probably due to "introgression."

The *parietal lamella* may be arcuate, sharply angular, slightly angular, or small and straight. The frequencies of these types are 39, 22, 26, and 13 per cent, respectively. The arcuate type is somewhat more frequent in the southern areas than in the northern.

Among the *measured characters*, shell width is correlated with height, umbilicus, and whorl number. All characters, including the graded ones, show irregular geographic variation; in a small area like that of *f. alabamensis* one cannot really expect any trend in geographic variation to develop.

Systematics. *Triodopsis f. alabamensis* was originally ranked by its author as a full species. The same investigator later ranked it, however, as a subspecies of *T. vannostrandi* (Pilsbry, 1912). This was a bad move, since *vannostrandi* is a hybrid between *alabamensis* and *f. fallax* or *f. obsoleta*, and is, therefore, an invalid name. Correctly, we should combine *alabamensis* with *fallax*, since they freely hybridize. Evidence for this statement is given below.

Hybrid populations between *f. alabamensis* and the *f. fallax-f. obsoleta* group

Plate III: 8, 12, 13

Populations from the transitional zone between *f. alabamensis*, *f. fallax*, and *f. obsoleta* have mean values of 45–65 in character index B; that is, values intermediate between those of *f. alabamensis* (20–40) and *f. fallax* or *f. obsoleta* (70–90). One population from Blountstown, Calhoun County, Florida, with a mean value of 70, is also listed among the intermediate populations, because of its geographic position.

These samples are considered hybrids between *f. alabamensis* and the *f. fallax-f. obsoleta* group. This view is supported by the facts that they are morphologically and geographically intermediate, and their variation is greater than that of samples taken

←

Figure 17. Distribution and the geographic variation of character index B of *Triodopsis fallax*. Thick, dashed line separates the ranges of *f. fallax*, *f. obsoleta*, and intermediates between the two subspecies; thick, solid line surrounds the range of *f. alabamensis* and hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies. Parallel, thin lines indicate a transect; thin, dashed lines are state boundaries. AFF., type locality of *affinis*; CHI., *chincoteagensis*; OBS., *f. obsoleta*; PAL., *palustris* (these four forms are all combined in *f. obsoleta*). FAL., *f. fallax*; ALA., *f. alabamensis*. CHA., *charlestonensis*; GON., *goniosoma*; MES., *messana*; VAN., *vannostrandi* (these four forms are all considered hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies). Numbers are mean values of samples in character index B. Samples of *f. alabamensis* range from 20 to 40, hybrid, 45–65, *f. fallax* and *f. obsoleta*, 70–90, intermediate between the latter two subspecies, 70–75.

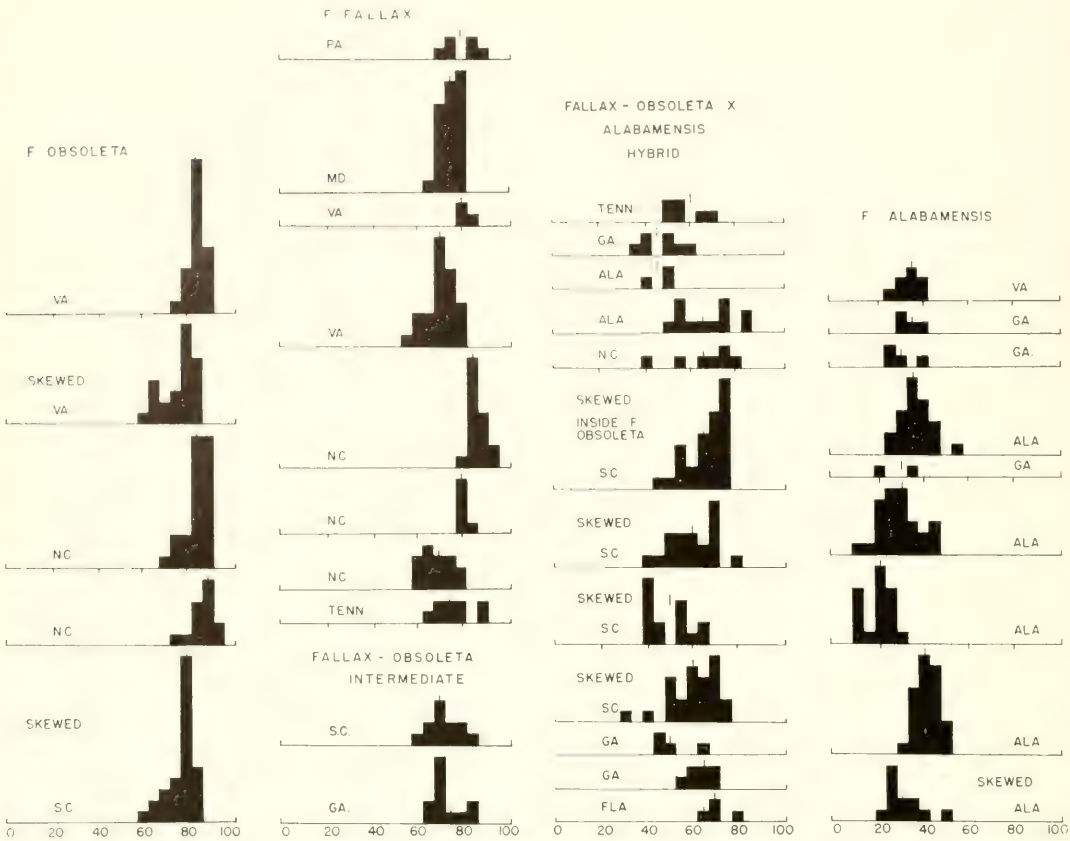

Figure 18. Character index B, histogram of samples of *Triodopsis fallax*. Short line on top of column indicates mean value of sample. The histograms of many hybrid samples are strongly skewed, those of the parental ones, normal or slightly skewed. The hybrid samples have a wider range of variation than do the parental samples. Samples of *f. alabamensis* also have a somewhat wider variation than do those of *f. fallax* or *f. obsoleta*. Scale in character index units. The abbreviations stand for the states where the samples have been collected.

from either of the putative parents (Figs. 4, 18, 26, 27).

The hybrid origin of the intermediate populations is further supported by the fact that the hybrid zone does not coincide with obvious changes in ecological factors, such as vegetation, elevation, temperature, humidity, or soil.

Hybrid populations have been *measured* from the following localities (Fig. 17): *North Carolina*: Wilkes and Columbus counties (ANSP). *Tennessee*: Campbell County (ANSP). *South Carolina*: Greenville County (MCZ); Aiken (2 samples), Bamberg, Marion, Charleston, and Beaufort counties (ANSP). *Georgia*: Clarke, Bibb, and Baker counties (MCZ). *Alabama*: Jackson County (MCZ); DeKalb and Jefferson counties (ANSP). *Florida*: Alachua and Calhoun counties (ANSP). A total of 18 samples, 1–30 specimens each, 162 specimens altogether.

The hybridization of *f. alabamensis* with *f. fallax* and *f. obsoleta* has several important effects on the taxonomy and nomenclature of the group. First, the former *T. alabamensis* must be considered conspecific with *f. fallax* and *f. obsoleta*. Second, the name *vannostrandi alabamensis* must be changed to *fallax alabamensis*. Third,

Figure 19. Geographic variation of whorl to width ratio in *Triodopsis fallax*. Thick, solid line separates the range of *f. fallax* and *f. obsoleta* from that of hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies; thick, dashed line separates the hybrids from *f. alabamensis*. Numbers without a circle are mean values of samples in whorl to width ratio; the samples of *f. fallax* range from 0.41 to 0.51; *f. obsoleta*, 0.42–0.48; intermediate, 0.46–0.50; hybrid, 0.47–0.58; *f. alabamensis*, 0.53–0.64. The variation of the character is irregular in all taxa. Numbers encircled refer to forest types (terminology after Fenneman, 1938): one, mainly coniferous forest; two, beech, birch, maple; four, chestnut, chestnut-oak, poplar; five, oak and pine; six, cypress, tupelo, red gum, river bottom forest; seven, prairie grassland with wooded valleys; eight, southeastern pine forest; nine, marsh grassland. Notice the "straits" of deciduous forests, chestnut, chestnut-oak, and poplar, between the "islands" of mainly coniferous forests; the former provided convenient routes of dispersal for several species of *Triodopsis* (p. 167). Elevation: ••••• 500-foot contour line; •••••• 1000-foot; • • • • • 1500-foot. Other symbols and abbreviations as in Figure 17.

the names previously given to the hybrid populations must not be used. There are five such names:

Helix hopetonensis Shuttleworth, 1852, Mitt. Naturforsch. Ges. Bern No. 248: 198. Hopeton, near Darien, Georgia. Cotype MCZ 18225.

Helix vannostrandi Bland, 1875, Ann. Lyc. Nat. Hist. New York 11: 200. Aiken, Aiken County, South Carolina. Type not seen. Topotypes ANSP 57196 and 86104.

Polygyra fallax subsp. *goniosoma* Pilsbry, 1912, Nautilus 26: 80. In oak and pine-woods, Blountstown, Calhoun County, Florida. Type ANSP 77948.

Polygyra hopetonensis var. *charlestonensis* Mazyck, 1913, Contrib. Charleston Mus. 11: 7. Charleston, Charleston County, South Carolina. Type ANSP 106850.

Triodopsis messana Hubricht, 1952, Nautilus 65: 80. Whiteville, Columbus County, North Carolina. Holotype ANSP 187456, paratypes 187455.

Hubricht (1953, *in litt.*) states that *fallax, hopetonensis, obsoleta* and *alabamensis* are separate species, isolated from one another by "geographical and ecological" factors or by a difference in the breeding season, and only hybridize where their natural habitats have been destroyed. He also stated that hybrid populations are only found in "disturbed" habitats, like vacant lots. From these observations he concluded that, "Prior to the coming of the white man to America, it is doubtful if they ever hybridized."

On the distributional map of the group (Figs. 15, 17) one cannot see any obvious geographic barrier between *f. fallax* and *f. obsoleta* or *f. alabamensis*. Hubricht also failed to tell where they are supposed to be. Ecological isolation may exist between *f. fallax* and *f. obsoleta*, but it is unlikely between these and *f. alabamensis*. The hybrid populations occur not only in disturbed habitats, but also in relatively undisturbed ones, such as national forests and state parks. In such habitats, "pure" populations are found outside of the hybrid zone. Furthermore, it is unlikely that habitat disturbance would occur only in the Georgia-Carolina region, where hybrids are found, and not in the Maryland-Washington-Virginia region, where *f. fallax* and *f. obsoleta* are sharply separated from one another. For all of these reasons, it seems doubtful to me that habitat disturbance is the only or even the major factor in the hybridization of the *fallax* group, although it may have helped to facilitate it.

Evolutionary relationships. Triodopsis f. fallax is most closely related to *f. obsoleta. Triodopsis f. alabamensis*, judged on a morphological basis, was separated from the *fallax-obsoleta* stock a long time ago; it has failed, however, to achieve reproductive isolation, and is therefore presently merging with this stock.

Summary. (1) *Triodopsis fallax* consists of three subspecies: *f. fallax, f. obsoleta* and *f. alabamensis*. The first corresponds to *T. fallax* of contemporary authors. The second combines the former *hopetonensis obsoleta, h. chincoteagensis, fallax affinis* and *palustris*. The third corresponds to the former *vannostrandi alabamensis*.

(2) *Triodopsis f. fallax* and *f. obsoleta* intergrade in the southern part of the range, but are sharply separated elsewhere (this may be the phenomenon referred to as "widening of the hybrid belt"). Because of this intergradation, *fallax* and *obsoleta* are considered conspecific; they both freely hybridize with *f. alabamensis*—a proof of conspecificity with that form. Habitat disturbance by man probably did not play a major role in initiating the hybridization.

(3) Judged by its heavy armature, *f. fallax* appears to be a mountain snail; in fact, however, it occurs at relatively low elevations. The reason for this anomalous distribution is not known.

(4) *Triodopsis f. fallax* and *f. obsoleta* are ecologically exclusive of *T. tridentata* and *T. j. juxtidens*.

(5) The geographic variation of most characters is irregular in all three subspecies. The aperture varies clinally, however,

TABLE X

CHART FOR COMPUTING CHARACTER INDEX FOR *TRIODOPSIS COPEI*. METHOD OF CALCULATION: A SPECIMEN HAVING A WIDTH OF 14.5 MM, AN UMBILICUS OF 3.5 MM, A WHORL TO WIDTH RATIO OF 0.42, AN APERTURE GRADE D, AND A LARGE FULCRUM SCORES $(50 + 30 + 40 + 40 + 40)/2 = 100$, THE MAXIMUM POSSIBLE SCORE.

SCORE	WIDTH IN MM	UMBILICUS IN MM	WHORL TO WIDTH RATIO	APERTURE GRADE	FULCRUM GRADE	
0	7.7–8.2	1.1–1.4	0.58–0.60	B	none	*c. cragini*
5	8.3–8.7	1.5–1.8	0.56–0.57			↑
10	8.8–9.3	1.9–2.2	0.54–0.55	B-C	questionable	↑
15	9.4–9.9	2.3–2.5	0.52–0.53			↑
20	10.0–10.5	2.6–2.8	0.50–0.51	C	small	↑
25	10.6–11.1	2.9–3.2	0.48–0.49			↑
30	11.2–11.7	3.3–4.0	0.46–0.47			↑
35	11.8–12.2		0.44–0.45			↑
40	12.3–12.8		0.41–0.43	D	large	↑
45	12.9–13.4					↑
50	13.5–14.5					*c. copei*

from *f. fallax* to *f. obsoleta*, and this cline corresponds to gradual changes in the environment, primarily in elevation. There is no clinal variation in *Triodopsis f. alabamensis*.

(6) *Triodopsis f. fallax* and *f. obsoleta* are very close relatives. Long ago, presumably, *Triodopsis f. alabamensis* split away, but is presently fusing with them.

Triodopsis copei (Wetherby)

The name *Triodopsis copei* supersedes the more commonly used *T. vultuosa*, for reasons to be explained below. Two hybridizing subspecies belong to the species: *c. copei* and *c. cragini*.

Triodopsis copei copei (Wetherby)

Plate III: 20

Helix copei, or *H. vultuosa* var. *copei* Wetherby, 1878, Amer. Nat. 12: 185. Twenty miles north of Beaumont, Jefferson County, Texas. Types ANSP 57222 and 82316.

Definition. *Triodopsis c. copei* is the former *T. vultuosa copei*. The populations that belong to this subspecies have mean values of 75–100 in character index. The method of computing character index is described in Table X.

Description. Shell width 11.5–14.5 mm; height 6.1–7.5 mm, height to width ratio 0.48–0.60; umbilicus 1.9–4.0 mm, umbilicus to width ratio 0.17–0.28; number of whorls 5.3–6.0, whorl to width ratio 0.41–0.50; embryonic whorls 1.4–1.5, with faint striation below suture; striation becoming more pronounced on later whorls, 3–5 striae per millimeter on last whorl; intervals of striae without papillae; aperture trapezoid, square, oval, or rarely auriculate; lip swelling thick and marginal or very slightly receding, therefore edge of aperture swollen; upper lip tooth very broad and deeply receding, lower lip tooth moderately large and marginal, often buttressed on its left side; parietal lamella large and angular; fulcrum moderate to large; moderate to large projection on face of lower lip.

Differential diagnosis. *Triodopsis c. copei* is very similar to *T. f. fallax*. The best distinction between them is that *c. copei* has a swollen peristome and a moderate to large projection on the lower lip, whereas *f. fallax* has a sharp peristome and a small projection.

Distribution. *Triodopsis c. copei* is known only from a limited area in southeastern Texas (Fig. 20). Its range is separated by a gap of several hundred miles from that of the related species *T. fallax*. The *measured material* comes from the following localities: *Texas*: Anderson, Houston, An-

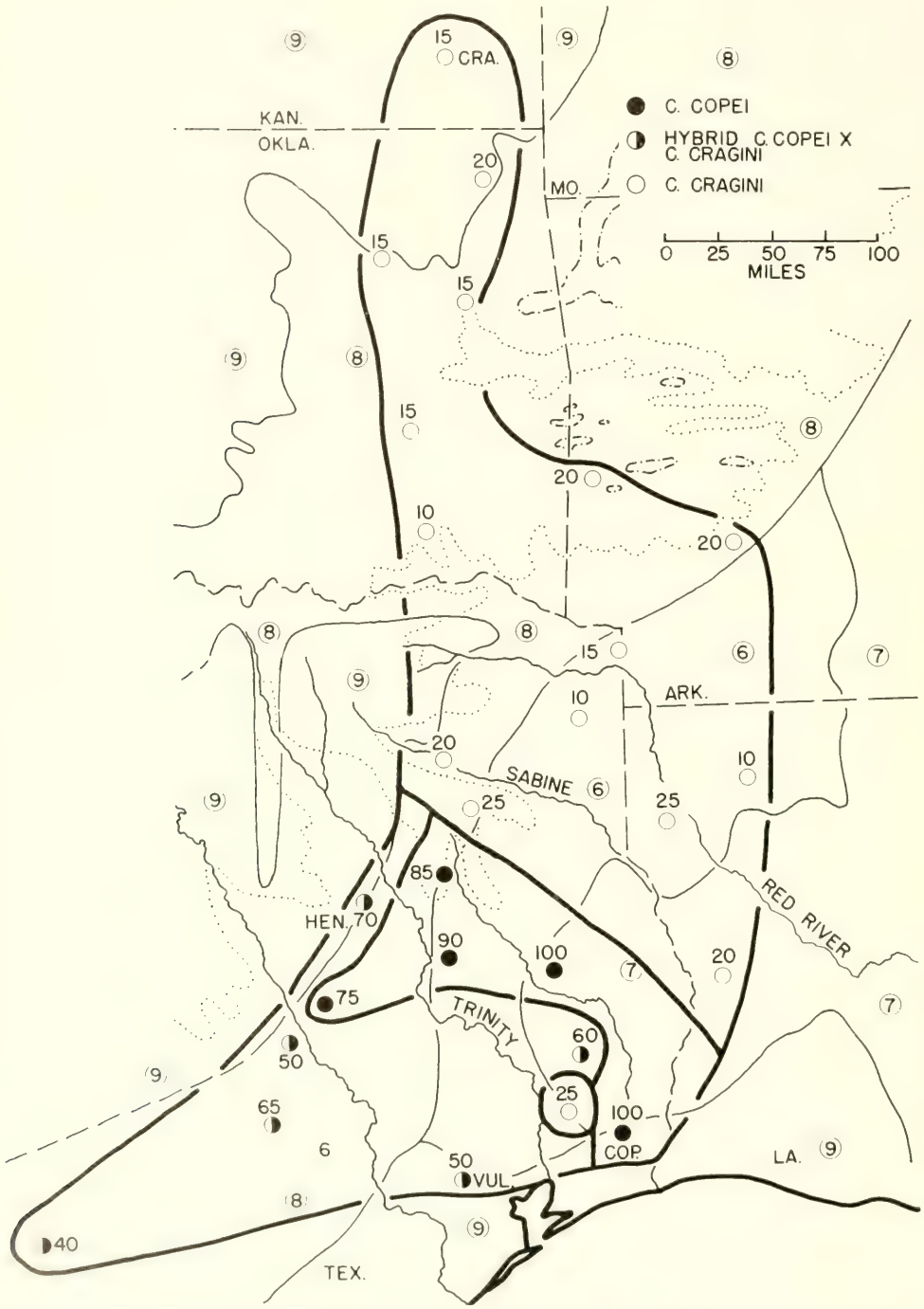

Figure 20. Distribution and the geographic variation of the character index in *Triodopsis copei*. Thick, solid line surrounds the range of c. *cragini*, c. *copei*, and hybrid c. *cragini* × c. *copei*. COP, type locality of c. *copei*; CRA, c. *cragini*; HEN, *henriettae*; VUL, *vultuosa*; the latter two forms are considered hybrid c. *cragini* × c. *copei*. Numbers without a circle are mean values of samples in character index; samples of c. *cragini* range from 5–35, hybrid, 40–70, c. *copei*, 75–100. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

gelina, and Jefferson counties (ANSP); Robertson County (MCZ). A total of 5 samples, 2–7 specimens each, 16 specimens altogether.

Ecology. Triodopsis c. copei occurs predominantly in oak-pine and southeastern evergreen forests, but it also penetrates the oak-hickory forests and grasslands (Fig. 20). It ranges from roughly 100 feet to about 500 feet elevation. This is very remarkable, in view of the fact that it has the large lip teeth and parietal lamella of a "mountain" snail. I cannot offer any satisfactory explanation for this anomaly.

Systematics. Triodopsis c. copei was originally described as a full species *or* a variety of *vultuosa*. Subsequently, it was ranked as either a variety or a subspecies of *vultuosa*. The type population of *vultuosa* is, however, a hybrid between *copei* and *cragini*; the name *vultuosa*, therefore, should not be used. The oldest available name for the species thus becomes *copei*, and the former *vultuosa copei* becomes *c. copei*.

Triodopsis copei cragini Call
Plate III: 16–18

Triodopsis cragini Call, 1886, Bull. Washburn College Lab. Nat. Hist. 1: 202, fig. 5. Banks of Chetopa Creek, Thayer, Neosho County, Kansas. Type MCZ 3123; paratypes MCZ 3124.

Definition. Triodopsis c. cragini is the former *T. cragini*. It comprises those populations of the species with mean values of 0–30 in character index. The method of computing character index is shown in Table X (p. 199).

Description. Shell width 7.7–10.8 mm; height 3.7–6.7 mm, height to width ratio 0.48–0.67; umbilicus 1.1–2.0 mm, umbilicus to width ratio 0.13–0.19; number of whorls 4.3–5.5, whorl to width ratio 0.47–0.60; embryonic whorls 1.4–1.5, feebly striated below suture, smooth elsewhere; striation becoming more pronounced on later whorls, 4–5 striae per millimeter on last whorl; aperture squarish to rounded; lip swelling moderately thick; lip teeth moderately large and angular; fulcrum usually absent, small if present; projection on face of lower lip small or absent.

Differential diagnosis. Triodopsis c. cragini is easy to distinguish from *T. c. copei* because its shell is smaller and more tightly coiled, and its armature is weaker. It is more difficult to distinguish from *T. f. obsoleta* or *f. alabamensis*. It is differentiated from the former by its square to rounded aperture and higher whorl to width ratio; from the latter it differs in having fewer whorls and a broader upper lip tooth. If we recall that *T. c. copei* resembles *T. f. fallax*, a parallelism between *T. copei* and *T. fallax* becomes evident. Both have evolved a large subspecies with heavy armature, and one or two small subspecies with light armature.

Distribution. Triodopsis c. cragini occurs in a narrow band running from Kansas to Texas and Louisiana, avoiding the Ozark Mountains (Fig. 20). In Texas it is contiguous with *T. c. copei*.

The *measured material* comes from the following localities: *Kansas*: Neosho County (MCZ). *Oklahoma*: Craig, Tulsa, Muskogee, Pittsburgh, and Pushmataha counties (ANSP). *Arkansas*: Polk, Clark, and Miller counties (ANSP). *Louisiana*: Bienville and Vernon counties (MCZ); De Soto County (ANSP). *Texas*: Cass and Wood counties (ANSP); Smith and Hardin counties (MCZ). A total of 16 samples, 2–12 specimens each, 83 specimens altogether.

The record from Muskogee County (ANSP 4718, Brown Collection) may be erroneous. These specimens have a much smaller and flatter shell than any other specimen of *c. cragini* seen. They look much like hybrid specimens between *T. f. alabamensis* and *f. fallax* or *f. obsoleta* from Alabama. Also, there is a Muscogee County in the neighboring state of Georgia. Only two specimens are available, however, which does not permit a certain identification. For this reason I tentatively included this sample in *c. cragini*.

Ecology. Triodopsis c. cragini inhabits oak-hickory, oak-pine, and southeastern evergreen forests seemingly without any preference (Fig. 20). A few localities fall in the grasslands. It is possible, however, that these localities also lie in small patches of woods that do not show up on the large scale map used here. *Triodopsis c. cragini* is found between about 100 and 1000 feet elevation. It is remarkable that it is found at higher elevations than *c. copei* because *T. c. copei* has the appearance of a mountain snail, whereas *c. cragini* does not. No explanation is known for this "reversed" distribution (p. 239).

Systematics. Triodopsis c. cragini was described as a full species. Subsequently, it was considered either a variety of *vultuosa* (Singley, 1893), or a synonym of *copei* (Binney, 1890). Finally, its specific status was restored (Pilsbry, 1901, 1940), on the grounds that it differs from *vultuosa* by its smaller size, lack of fulcrum, and lack of the projection on the lower lip, and because Pilsbry believed there was no intergradation between them. As shown below, however, intergradation does occur. The specific status of *cragini* is therefore not warranted; correctly, we should consider it a subspecies conspecific with *copei*. Thus the name used in this paper: *T. copei cragini*.

Hybrid populations between *Triodopsis* c. *copei* and c. *cragini*

Plate III: 19

Some populations are intermediate between *T. c. copei* and *c. cragini* in morphological characters. This is expressed by their mean values in character index, which vary between 40 and 70. (The mean values of *c. cragini* range from 5 to 35, those of *c. copei* from 75 to 100.)

Such populations are known from the following localities: *Texas*: Freestone, Milan, Lee, Bexar, and Harrison counties (ANSP); Tyler County (MCZ). A total of 6 samples, 2–21 specimens each, 55 specimens altogether. The localities lie mainly in forested area, between 100 and 500 feet elevation (Fig. 20). However, one of the non-measured samples comes from "fields along top of hill . . . near entrance of ship channel into Galveston Bay" (ANSP 187-087).

The variation in character index of the intermediate populations is about normal, except for the population from Freestone County, which has much wider variation than any other sample of the species. On this basis, the former samples appear to be primary intergrades, the latter one a secondary intergrade or hybrid. It seems unlikely, however, that such a dual explanation could be true. It is more probable, for several reasons, that all intermediate populations are hybrids. First, there is great similarity between the distributional pattern of *T. copei* and the related species, *T. fallax*. In both species, the intermediate populations surround the southern subspecies (Figs. 17 and 20). Presumably, the evolutionary history of the two species is similar. Since the intergrades are hybrids in *fallax*, they may be hybrids in *copei*, also. Second, it is difficult to see how primary intergradation (variation) could explain the occurrence of intermediate populations around the range of *c. copei*. Immigration of *c. cragini* into the peripheral zone of the range of *c. copei*, and subsequent hybridization, explains this pattern better. Third, the existence of a sharp character gradient between *c. copei* and *c. cragini* also indicates secondary intergradation, as discussed in more detail below.

Not all intermediate populations show increased variation; this can be attributed to the fact that the populations available for comparison are too small. Character displacement cannot explain the existence and distribution of the intermediate populations, because *c. copei* and *c. cragini* do not overlap. Because they demonstrate the conspecificity of *copei* and *cragini*, these intermediate populations are of great significance.

The paratype specimen of *vultuosa*[1] closely approximates the hybrid specimens. The available specimens of another recognized form, *henriettae*,[2] also seem to be hybrids. It is proposed, therefore, that these names be no longer used, and that the name of the species under discussion be changed from *vultuosa* to *copei*.

Variation in Triodopsis copei. As *T. c. copei* and *c. cragini* are within the same spectrum of variation, it is justified to discuss them together in this section.

Aperture: Three grades of aperture can be distinguished according to the degree of development of the armature. These are referred to as aperture grades B, C, and D. Aperture grade A was omitted, because specimens comparable to grade A of *T. fallax* (very weak armature) do not occur in this species, and it is desirable to keep the nomenclature consistent. Specimens of aperture grade B have a moderately thick lip swelling, moderately large lip teeth and parietal lamella, and a narrow to moderately broad upper lip tooth (Plate III). The lip teeth and parietal lamella do not obstruct the aperture. The lip swelling in grade C is thicker, the lip teeth and parietal lamella larger, and the upper lip tooth broader than in grade B, and these structures obstruct the aperture to a degree. In grade D, the lip swelling is thick, the lip teeth and parietal lamella very large, and the upper lip tooth very broad; the aperture is greatly obstructed. Intergradation between the various grades occurs.

In a given population usually only one grade is found, but in some cases B mixes with C, or C with D. Populations made up solely of grade B specimens are classified as *c. cragini*, B + C populations as *c. cragini* or hybrid, C as hybrid, C + D as hybrid or *c. copei*, and D populations as *c. copei*. The final decision in the case of the B + C and C + D populations is based on other characters.

Aperture grade B occurs predominantly in the northern and eastern parts of the range, D in the center of the southern part of the range, and C around the latter. This, of course, corresponds to the distribution of the two subspecies and the hybrids.

Fulcrum: This may be large, small, or absent. The absence of a fulcrum is a characteristic of specimens of aperture grade B, a small fulcrum of grade C, and a large fulcrum of D. Occasionally, however, a small fulcrum may occur in grade B, and a large one or none in C.

Measured characters: Height and umbilicus are correlated with width (size). Whorl number is also correlated with width within each subspecies, although *c. cragini*, of smaller dimensions, has relatively more whorls than *c. copei*. The measured characters are, to an extent, also correlated with aperture grades and the development of the fulcrum. Smallest and lowest are specimens of aperture grade B, larger and higher of grade C, etc. The geographic variation of the measured characters shows basically the same pattern as the character index.

Character index: Shell width (size), umbilicus, whorl to width ratio, aperture grade, and fulcrum grade were utilized in preparing the character index (Table X). The mean values of populations in character index are uniformly low in the northern and eastern parts of the range (Fig. 20). A high "plateau" of character index occurs in the southern-central region. Intermediate character index values surround the high plateau with the exception of the northeast; here the high values directly confront low ones, thus forming a very sharp character gradient.

This gradient runs from northwest to southwest, across eastern Texas, following

[1] *Helix vultuosa* Gould, 1848, Proc. Boston Soc. Nat. Hist. 3: 39. As type locality, Gould gave "Arkansas and Texas." The examined paratype, ANSP 187539, is most similar to specimens from Houston, Harris County, Texas. On this basis the type locality is here restricted to Houston.

[2] *Helix* (*Triodopsis*) *henriettae* Mazyck, 1877, Proc. Acad. Nat. Sci. Philadelphia, p. 297. "Eastern Texas." Type not seen.

no apparent physiographic barrier. The Sabine and Neches rivers, which run parallel with the gradient only a short distance away, scarcely qualify as barriers. It seems likely, therefore, that historical factors are responsible for the sharpness of the gradient. Presumably, the populations that presently confront each other developed their differences in isolation; their present contact is secondary.

Systematics. *T. copei* could be regarded either as conspecific with *T. fallax* or as a separate species. It is not known whether the two are reproductively isolated. Because *f. alabamensis* (which is morphologically less similar to *f. fallax* or *f. obsoleta* than are *c. copei* or *c. cragini*) can interbreed with *f. fallax* and *f. obsoleta*, it might be assumed that *c. copei* and *c. cragini* also can. Hence, we could consider *copei* and *fallax* conspecific. The method of estimating the potentiality of interbreeding has, however, repeatedly proved erroneous (p. 232). Also, both species have already split into several subspecies. I think, therefore, that *copei* and *fallax* should not be combined in one species.

Evolution. On morphological grounds it seems certain that *T. copei* developed from the same stock as *T. fallax*. The subsequent evolution of the two species proceeded along parallel lines. Both have produced a "mountain" and one or two "lowland" subspecies. The situation in *T. copei* is complicated, however, by the fact that the "mountain" subspecies only looks that way, and in fact occurs in lower areas than the supposed lowland subspecies does. We cannot tell, therefore, what forces can possibly be held responsible for the development of the two subspecies.

Summary. (1) *Triodopsis copei* corresponds to the *vultuosa-cragini* complex of contemporary authors. It is divided into two subspecies: *c. copei* and *c. cragini*. The first corresponds to the former *vultuosa copei*, the second to *cragini*. The two subspecies intergrade; this intergradation is presumably secondary (hybridization). Two of the hybrid populations, *T. v. vultuosa* and *T. v. henriettae*, are considered separate subspecies by contemporary workers.

(2) The range of *T. c. copei* is contiguous with that of *c. cragini*; the hybrid populations surround the range of the former. This pattern is not correlated with any physiographic feature.

(3) *Triodopsis c. copei* occurs at low elevations. This is not in accordance with its heavy armature, which is typical of mountain species. *Triodopsis c. cragini* ascends to somewhat higher elevations.

(4) The geographic variation is irregular within each subspecies.

(5) On morphological grounds it can be assumed that *T. copei* evolved from the same ancestor as *T. fallax*, and developed along parallel evolutionary lines with that species.

Triodopsis soelneri (J. B. Henderson)

Polygyra soelneri J. B. Henderson, 1907, Nautilus 21: 13, pl. 3, figs. 1–2. Among cypress logs on the north shore of Lake Waccamaw, Columbus County, North Carolina. Type ANSP 94682.

Definition. *Triodopsis soelneri* is recognized here as defined by its author.

Description. The description is based partly on Henderson's original description (1907), on Pilsbry's (1940) and Hubricht's (1950a) data, and partly on my own measurements.

Shell width 10.0–11.0 mm; height 6.3–7.2 mm; umbilicus very narrow, partially covered by reflection of lower lip; number of whorls 5.5; embryonic whorls 1.5, finely striated below suture, smooth otherwise, subsequent whorls with strong striae and, in the intervals of striae, with papillae; papillae scarce except in umbilical region where numerous; aperture oblique-oval; lip swelling bladelike, but becoming obsolete near junction of lower lip with shell; upper lip tooth small or absent, lower lip tooth absent; parietal lamella long and slightly bent.

Differential diagnosis. The bladelike lip swelling which usually does not bear any tooth, the partially covered umbilicus, the

small dimensions of the shell, and the lack of complex sculpture readily distinguish *soelneri* from the species of the *T. obstricta* group, to which it shows superficial similarities.

Distribution. In addition to the type locality, Lake Waccamaw, Columbus County, North Carolina, Hubricht (1950a, 1953) has reported *T. soelneri* from Bladen, Brunswick, and Jones counties, all in North Carolina.

Ecology. The type locality was a cedar swamp on the northern shore of Lake Waccamaw. As Hubricht reports, this area has been drained and is being built on; he predicts that the type population will soon be exterminated. A second type of habitat in which *soelneri* is found is pine woods (Hubricht, 1953). The pine woods specimens, according to Hubricht, are smaller and have "a small but distinct denticle on the outer [upper] lip."

T. soelneri has been found coexisting with *T. hopetonensis* and *T. messana* (considered hybrids between *f. fallax*, *f. obsoleta*, and *f. alabamensis* in this paper [p. 198]).

The range of variation of *Triodopsis soelneri* is very narrow, probably because of its limited area of distribution and small population size.

Systematics. As Pilsbry pointed out (1940: 815), *T. soelneri* "is a somewhat isolated snail, as near to *T. hopetonensis* as to any of the fully toothed species. This estimate of its affinities is confirmed by the structure of the penis, the fleshy body within the upper cavity being similar to that of *hopetonensis* but much shorter. . . ."

Summary. *Triodopsis soelneri* is an isolated species within the *fallax* complex. It occurs in a restricted area. Its range of variation is narrow.

Subgenus *XOLOTREMA*

Xolotrema Rafinesque, 1819, J. Phys. Chim. Hist. Nat., 88; *non Xolotrema* Rafinesque, 1831.

Type. Triodopsis o. denotata, designated by Pilsbry (1940: 823).

The shell is usually larger than in the subgenus *Triodopsis*, imperforate, and with a characteristic sculpture. The aperture has a long, bladelike lamella in the lower lip instead of a lip tooth.

The subgenus contains only one species complex, *obstricta.*

Rafinesque did not designate a type species for *Xolotrema.* Furthermore, he used the term in two different ways, in 1819 and 1831. Pilsbry (1940: 823) clarified the meaning of the term *Xolotrema*, and designated *T. notata* (in this paper called *T. obstricta denotata*) as type species. Pilsbry's reasoning was that *T. o. denotata*, as well as all the other forms included in the *obstricta* complex, is recognizable from Rafinesque's 1819 description of *Xolotrema* as belonging to the genus, and is thus available as the type species. Rafinesque's 1831 description of *Xolotrema* refers to the *Mesodon inflectus* group.

The *obstricta* Complex

This complex contains two well-distinguished species: *Triodopsis obstricta*, with subspecies *o. obstricta* and *o. denotata*, and *T. fosteri*, with subspecies *f. fosteri* and *f. hubrichti.* The two subspecies of *T. obstricta* hybridize. The separation of two subspecies of *T. fosteri* may not be warranted.

Triodopsis obstricta (Say)
Triodopsis obstricta obstricta (Say)
Plate IV: 5, 6

Helix obstricta Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 145. "Inhabits Ohio." There is a specimen in the ANSP, 11271, labelled as "Probably the type," from Ohio. This is probably in error, however, since *obstricta* seems not to occur in Ohio (see systematics). I therefore restrict the type locality to Murfreesboro, Rutherford County, Tennessee, which falls within the range of the subspecies.

Carocolla helicoides Lea, 1834, Trans. Amer. Philos. Soc. 4: 103, pl. XV, fig. 34a–c. Near Nashville, Davidson County, Tennessee. Type not seen.

Definition. Triodopsis o. obstricta corresponds to *T. obstricta* of Pilsbry (1940),

TABLE XI

CHART FOR COMPUTING CHARACTER INDEX IN *TRIODOPSIS OBSTRICTA*. METHOD OF CALCULATION: A SPECIMEN WITH SCULPTURE D AND ANGULARITY TYPE 4 IS SCORED 55 + 45 = 100, THE AVAILABLE MAXIMUM SCORE.

SCORE	SCULPTURE	ANGULARITY	
0	A	1	*o. denotata*
5	A′		
10	B		
15		2	
20			
25			
30	C	3	
35			
40			
45		4	
50	D′		
55	D		*o. obstricta*

less *T. o. occidentalis*. It contains those populations of the species which have mean values of 80–100 in character index. The method of computing character index is shown in Table XI.

Description. Shell width 19.7–25.9 mm; height 9.6–12.6 mm, height to width ratio 0.41–0.56; umbilicus covered or nearly so; number of whorls 5.2–5.8, whorl to width ratio 0.22–0.27; embryonic whorls 1.4–1.5, finely striated; subsequent whorls with stronger striation; last whorl with very strong striae on upper side, weak striae on under side; intervals between striae or ribs with closely set, fine wrinkles running in a transverse, oblique, or spiral direction; transverse wrinkles often arranged in spiral rows; last whorl with prominent keel along its periphery; aperture oval; lip swelling thick, with a flat or concave face; upper lip tooth well developed, flat; lower lip tooth replaced by a long, bladelike lamella, running to columellar wall; parietal lamella long, low, slightly curved, pointing above upper lip tooth.

Distribution. *Triodopsis o. obstricta* is confined to the Cumberland Mountains of eastern Tennessee and adjoining Alabama (Fig. 21). The *measured material* comes from the following localities: *Tennessee*: Pickett, Overton, Davidson, Rutherford, Grundy, Franklin, and Maury counties (MCZ). *Alabama*: Jackson (2 samples) and Madison counties (2 samples) (MCZ). A total of 11 samples, 2–7 specimens each, 41 specimens altogether.

Ecology. The range of *T. o. obstricta* is mountainous, but never exceeds 1500 feet elevation. It is covered by mixed and western mesophytic forests (Fig. 21). Its eastern boundary runs parallel with the 1500-foot contour line, but elsewhere the boundaries do not correspond to physiographic features.

Systematics. Say gave "Ohio" as the type locality of *T. o. obstricta*. This was probably in error, however, since *o. obstricta* is not known from Ohio (except Taft's record, 1961, from Pickaway County, which is probably a hybrid between *o. obstricta* and *o. denotata*). Say's specimen agrees well with those from Tennessee. On this basis, I restrict the type locality to Murfreesboro, Rutherford County, Tennessee. If this interpretation is correct, *C. helicoides* must be considered synonymous with *o. obstricta*.

A population from the Ozark Mountains has been described by Pilsbry and Ferriss (1907) as *T. o. occidentalis*. Under the microscope, however, these shells show the papillate sculpture of *Mesodon sargentianus*, and therefore must be placed with that species.

Triodopsis obstricta denotata (Férussac)
Plate IV: 1, 4, 12

Helix palliata Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 152. "Illinois." Non *Helix palliata* Hartmann, 1807. Type ANSP 11256.

Helix denotata Férussac, 1821, Tableaux Systematiques des Animaux Mollusques, p. 34, no. 102 (*nomen nudum*). *H. denotata* is cited as a synonym of *palliata* in Férussac and Deshayes: Histoire Naturelle des Mollusques Terrestres et Fluviatiles, 1820–1851, p. 144, pl. 49a, fig. 5.

Helix notata "Fér." Deshayes, 1832, Encyclopédie Methodique Histoire Naturelle des Vers, par Bruguière et de Lamarck, continuée par G. P. Deshayes, Vol. 2, part C-MYT, p. 224. "Kentucky." Type not seen.

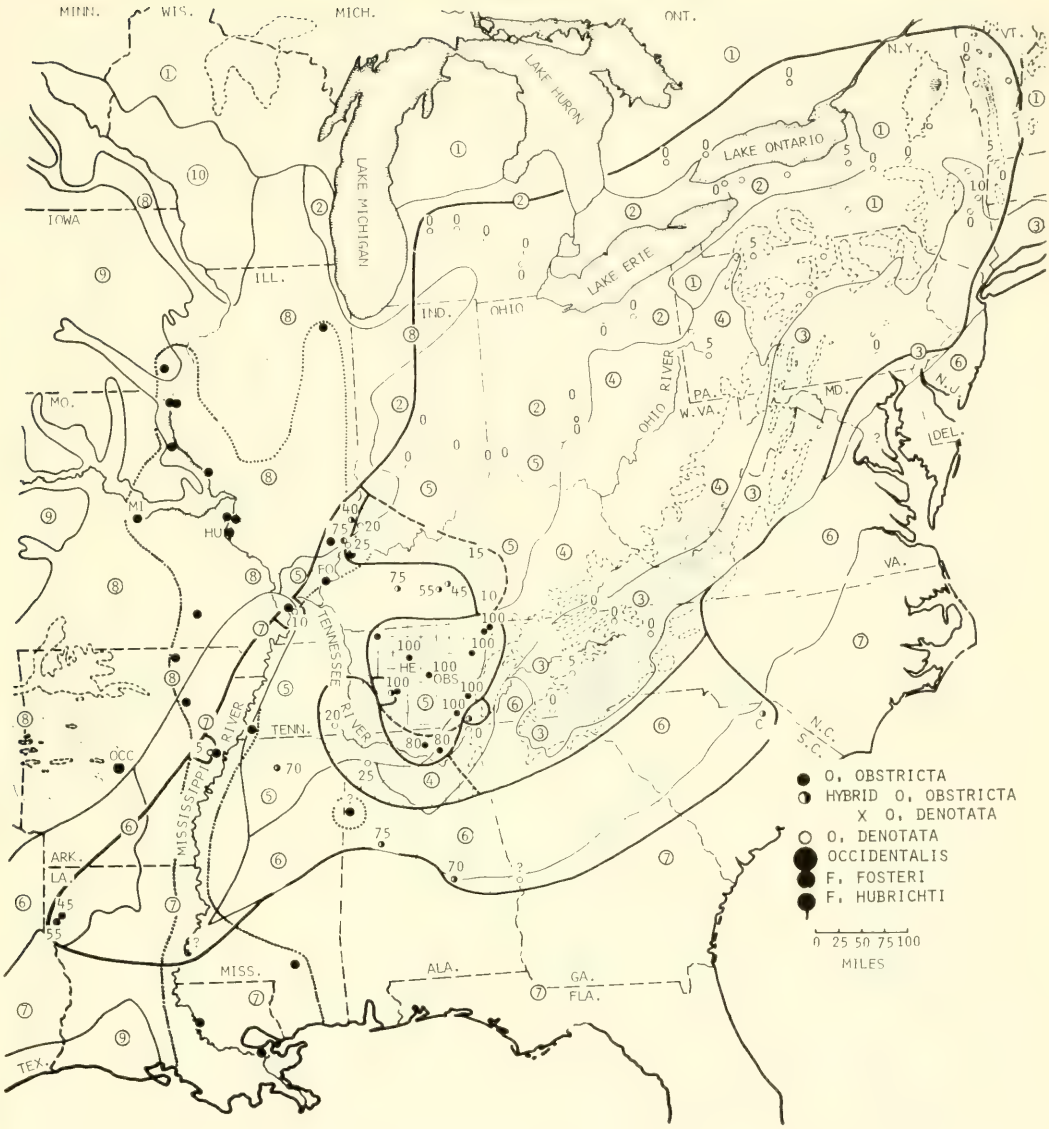

Figure 21. Distribution of *Triodopsis obstrica* and *fosteri*, and the geographic variation of the character index in *obstricta*. Thick, solid line surrounds the range of o. *obstricta*, o. *denotata*, and hybrids between the two subspecies; thick, dashed line, those peripheral areas of the range where limited interbreeding took place; dotted line surrounds the range of *fosteri*. Question mark beside a symbol means uncertain locality record. C., type locality of *caroliniensis*, considered hybrid o. *obstricta* × o. *denotata*; HE., *helicoides*, considered synonymous with o. *obstricta*; OBS., o. *obstricta*; OCC., *occidentalis*, considered synonymous with *Mesodon sargentianus*; FO., *f. fosteri*; HU., *f. hubrichti*; MI., *missouriensis*, considered synonymous with *f. fosteri*. Numbers without a circle are mean values of samples in character index; the samples of o. *denotata* range from 0 to 25, hybrid 40–75, o. *obstricta*, 80–100. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Definition. *Triodopsis o. denotata* corresponds to *T. notata* of Pilsbry (1940: 824), who combined *notata*, *denotata*, and *palliata*. It combines those populations of the species which have mean values of 0–25 in character index (Table XI).

Description. Shell width 17.0–25.9 mm; height 8.5–12.9 mm, height to width ratio 0.42–0.57; umbilicus completely or partially covered; number of whorls 4.8–5.8, whorl to width ratio 0.21–0.30; embryonic whorls 1.4–1.5, striated; striation becoming more pronounced toward aperture; intervals between striae with triangular scales; space between scales with fine, transverse wrinkles; last whorl angular or obtusely angular at its periphery; aperture oval; lip swelling well developed, flat; upper lip tooth also well developed, flat; lower lip tooth replaced by a long, bladelike lamella; parietal lamella long, low, slightly curving, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis o. denotata* is readily distinguishable from *T. o. obstricta* because of its scaly sculpture and weaker striation, and because it lacks a keel on the periphery of the last whorl.

Distribution. *Triodopsis o. denotata* ranges from Michigan and New Hampshire in the north to Alabama and Georgia in the south. Isolated populations also occur outside of this range, in Tennessee, Arkansas, and Louisiana (Fig. 21).

The *measured material* (all MCZ) comes from the following localities: *Ontario*: Hastings, Wellington, York, and Lincoln counties. *Vermont*: Chittenden and Bennington counties. *Massachusetts*: Berkshire County. *New York*: Dutchess, Columbia, Herkimer, Madison, and Onondaga counties. *Michigan*: Kent, Oakland, Washtenaw, Ingham, and Ionia counties. *Pennsylvania*: Lancaster, McKean, and Allegheny counties. *Ohio*: Summit, Lorain, Franklin, Pickaway, and Hamilton counties. *Indiana*: Marion, Dearborn, Decatur, Monroe, Gibson, and Posey counties. *Maryland*: Plummer Island (?county). *Virginia*: Lee County. *North Carolina*: Avery and Cherokee counties. *Kentucky*: Casey and Marion counties. *Tennessee*: Sullivan, Sevier, and Hardin counties. *Alabama*: Jackson and Franklin counties. A total of 42 samples, 2–24 specimens each, 197 specimens altogether.

Ecology. *Triodopsis o. denotata* occurs in various kinds of deciduous forests, predominantly between 500 and 1500 feet elevation (Fig. 21). Only a few localities occur below 500 feet. These populations were perhaps carried down by the streams, as is the case in *T. j. juxtidens*, *T. fraudulenta*, and *T. m. mullani*. We found *T. o. denotata* in greater abundance on the banks of creeks than high up on the hills. On the hills it coexists with *T. tridentata*; it does not seem to coexist, however, with the related species *T. fosteri*.

Systematics. Under *T. notata*, Pilsbry combined *palliata*, *denotata*, and *notata*. The first name is a homonym, and therefore cannot be used. *Helix denotata* Férussac, 1821, was published before *notata* Férussac, 1832 (see synonymy), but without a description. On this basis Pilsbry (1940: 824) called the taxon *notata*. But, as Pilsbry himself pointed out (1948: 1100), *denotata* was cited by Férussac in 1823 as equal to *palliata*; thus *denotata* is the valid name.

Some authors treat *T. o. denotata* as a full species, neglecting the intergradation that exists between this form and *o. obstricta*. I believe that because intergradation (hybridization) occurs, the two forms must be considered conspecific.

Hybrid populations between *Triodopsis o. obstricta* and *o. denotata*

Plate IV: 2, 3

Some populations are morphologically intermediate between *T. o. obstricta* and *o. denotata*; the mean values of these populations in character index range from 40–75, of *o. obstricta* from 80–100, of *o. denotata*, 0–25. Intermediate populations are known from an almost complete ring around the range of *o. obstricta* (Fig. 21). The *mea-*

sured material (all MCZ) comes from the following localities: *Indiana*: Posey County. *Illinois*: Wabash County. *Kentucky*: Hart, Edmonson, and Ohio counties. *Alabama*: Elmore and Tuscaloosa counties. *Mississippi*: Lafayette County. *Louisiana*: De Soto County (2 samples). A total of 10 samples, 2–5 specimens each, 28 specimens altogether.

The intermediate populations appear more variable than the populations of *T. o. obstricta* or *o. denotata*, so that they may be considered hybrids between the two subspecies. This interpretation is consistent with the fact that the intermediate populations are found in a zone that lies between the two subspecies, and on the periphery of the range of *o. obstricta* (see also p. 237).

One of the hybrid populations, from South Carolina, has been described as *Triodopsis caroliniensis*.[1] This name is placed, according to the rules, in the synonymy.

The hybrid populations show that *T. o. obstricta* and *o. denotata* are not isolated reproductively, and can thus be combined in one species.

Variation in Triodopsis obstricta. The variation of several characters is continuous through the two subspecies. It is, therefore, best to discuss the variation of both subspecies together.

Sculpture: Four types can be distinguished, referred to as A, B, C, and D. Shells of type A are moderately striated. In the spaces between the striae, large, triangular scales are found, arranged in oblique rows. From the base of each scale several short and thick wrinkles radiate out, dividing the shell surface into small polygons. The latter, in turn, are covered by very fine wrinkles, running in a transverse direction (Pl. IV, fig. 12). Type B resembles A closely, but the thick wrinkles may fuse to long, jagged lines. Type C is a mixture of A and D, and therefore will be described after D. Type D has very strong striae, almost like ribs. The fine sculpture consists of short wrinkles or lines, running in transverse, oblique, or spiral directions. When transverse, the fine wrinkles may be arranged in spiral rows. In type C, the polygonal sculpture and the scales of A occur together with the wrinkled sculpture of D; e.g., the upper side of the last whorl may be covered by short lines, the under side by polygons and very fine transverse wrinkles. Another type of sculpture also was considered C. This is a network of relatively thick, long wrinkles, in the meshes of which are visible short, transverse wrinkles. The striae in both types of C are as strong as in D.

Type A is characteristic of *T. o. denotata*, D of *o. obstricta*. Type B and type C occur in the hybrids and occasionally in some non-hybrid specimens. Type A is, accordingly, common in the northern half of the range, D in eastern Tennessee, B and C northwest, west, and south of the area of D.

Angularity of the last whorl: Four types can be distinguished, referred to as 1, 2, 3, and 4 (Plate IV). In 1, the periphery of the last whorl is rounded or bluntly angular, in 2 it is angular, in 3 sharply angular, without a keel, and in 4 sharply angular, with a keel. Type 1 is characteristic of *o. denotata*, 2 and 3 of the intermediates, and 4 of *o. obstricta*. Type 2 also occurs sporadically in otherwise "pure" populations of *o. denotata*.

Measured characters: Shell width is correlated with height and number of whorls. All measured characters show irregular geographic variation.

Character index: This was prepared by assigning numerical values to the various types of sculpture and angularity of the last whorl, and summing up these values. Thus a specimen of sculpture type A and angularity type 1 was scored $0 + 0 = 0$, etc. (Table XI).

The mean values of populations in char-

[1] *Triodopsis caroliniensis* Lea, 1834, Trans. Amer. Philos. Soc. 4: 102, pl. 15, figs. 33a–c. Cheraw, Chesterfield County, South Carolina. Type ANSP 11267.

acter index range from 0 to 100. Low values, between 0 and 25, correspond to *o. denotata*, high values, between 80 and 100, to *o. obstricta*, intermediate values, between 40 and 75, to hybrids. Populations with extremely low values are found in the northern and eastern parts of the range (Fig. 21). Populations with high values of 80–100 occur in eastern Tennessee, those with intermediate values northwest, west, and south of the latter. The change from low to high values is generally abrupt, but particularly so on the eastern side of the area of high values, where populations with mean values of 100 confront others with values of 0.

As to the origin of this pattern, we may put forward the following hypothesis. The differences between the two subspecies developed while they were isolated from one another. The intergradation between them is secondary, due to hybridization. The northern subspecies, *o. denotata*, invaded the periphery of the range of the southern subspecies, *o. obstricta*, and in places made quite deep inroads in it. In the invaded areas, hybridization is going on. In only one place did *o. denotata* not invade: in the east, where the Cumberland Mountains guard the eastern border of *o. obstricta*. Here hybrids are missing, and the "transition" from *o. denotata* to *o. obstricta* is sharp.

It seems unlikely that the above pattern of variation could be explained by primary intergradation. Should that be the case, we would expect the variation to reflect the physiographic pattern of the area, which it does not. Character displacement is almost certainly not involved, either. In character displacement, the most distinct populations should occur in the zone of overlap, the least distinct, outside. In this case, however, the distribution is just the reverse.

Summary. (1) *Triodopsis obstricta* is divided into two subspecies: *o. obstricta* and *o. denotata*. The two subspecies intergrade with each other, and the intergradation is presumably secondary. One of the intergrading (hybrid) populations has been mistakenly described as a separate species, *T. caroliniensis*. The currently recognized subspecies *T. o. occidentalis* is to be placed with *Mesodon sargentianus* as a synonym.

(2) *Triodopsis o. denotata* has a northern distribution, *o. obstricta* a southern one. The hybrid populations form an almost complete ring around the southern subspecies.

(3) *Triodopsis o. denotata* possibly shows ecological exclusion with *T. fosteri*.

(4) Both subspecies show irregular geographic variation.

Triodopsis fosteri (F. C. Baker)
Triodopsis fosteri fosteri (F. C. Baker)
Plate IV: 7–9

Polygyra appressa var. *fosteri* F. C. Baker, 1932, Nautilus 46: 48. Three miles northwest of Elizabethtown, in valley of Big Creek, Hardin County, Illinois. Paratypes ANSP 157437 and MCZ 92462.

Triodopsis fosteri forma *missouriensis* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 833, fig. 487i,j. Jefferson City, Cole County, Missouri. Type ANSP 11289; paratypes ANSP 168631.

Definition. Triodopsis f. fosteri includes the former *T. f. fosteri* and *f. missouriensis*.

Description. Shell width 13.8–22.0 mm; height 6.9–11.0 mm, height to width ratio 0.43–0.58; imperforate; number of whorls 4.6–5.5, whorl to width ratio 0.25–0.35; whorls flat, periphery of last whorl slightly angular; embryonic whorls 1.4–1.5, striated; striation becoming coarser toward aperture; 3 striae per millimeter on last whorl; space between striae with fine spiral threads; very short and very fine transverse wrinkles between spiral threads; details visible only on a fresh shell, under magnification of 25 × or higher; aperture oval; upper lip tooth small or lacking; lamella replacing lower lip tooth also small or lacking; parietal lamella moderately or well developed.

Differential diagnosis. Triodopsis f. fosteri is easily separated from *T. o. obstricta* and *o. denotata* by its smaller size, charac-

teristic sculpture, tighter coiling and weaker dentition. It is very similar, however, to *Mesodon appressus*; in fact, it was originally described as a subspecies of that form. The microscopic sculpture safely separates them, however; *Mesodon appressus* has regularly arranged papillae, or the shell is almost smooth. *Triodopsis f. fosteri*, on the other hand, has spiral threads and transverse wrinkles as described above. In addition, its shell is less flat than that of *appressus*.

Distribution. Triodopsis f. fosteri ranges from Iowa to Indiana in the east, and to Louisiana and Alabama in the south (Fig. 21). It was introduced in Burlington, New Jersey, in the 1860s by W. G. Binney. It established a thriving colony there. The Louisiana sample is actually labelled as Baton Rouge, Florida. I changed the state to Louisiana, because there is no Baton Rouge in Florida, and *f. fosteri* does not occur in that state.

The *measured material*, all MCZ, comes from the following localities: *Iowa*: Henry, Des Moines, and Lee counties. *Illinois*: Will, Hancock, Calhoun, St. Clair, Monroe, White, and Hardin counties. *Missouri*: Marion, St. Louis, and Carter counties. *Kentucky*: Ballard County. *Tennessee*: Shelby County. *Arkansas*: Sharp, Jackson, and Lee counties. *Alabama*: Lamar County. *Louisiana*: Orleans and East Baton Rouge counties. A total of 23 samples, 2–12 specimens each, 116 specimens altogether.

Ecology. Triodopsis f. fosteri is essentially confined to the Mississippi Valley (Fig. 21). It is seldom found over 500 feet elevation. Its range is covered by southeastern evergreen forests, on the alluvial plane of the Mississippi, or by oak-hickory forests, farther north. But it also invades the periphery of the grasslands and the western mesophytic forests.

In the Mississippi Valley, at Valmeyer, Monroe County, Illinois, we found *T. f. fosteri* living in great abundance on and at the foot of limestone bluffs that border the flood plains. We did not find any *T. o. denotata*, a related species that also occurs in the region, coexisting with it. This seems to indicate that the two species are ecologically exclusive of each other, but one observation is not sufficient to establish this conclusion definitely.

Variation. Sculpture: In three shells, deeply incised, spiral grooves replace the spiral threads in a part of the last whorl. This type of sculpture is probably the result of an injury to the shell, or, more accurately, to the mantle edge that produces the shell. In these three cases observed, the initial whorls bore normal sculpture, and the deep grooves appeared after a scar. Only single specimens showed such deep grooves, never whole demes. Several species of the subgenera *Neohelix* and *Cryptomastix* also show this phenomenon (p. 225, Pl. V, fig. 11).

Measured characters: Width of shell is correlated with height and whorl number. All characters show irregular geographic variation.

Systematics. Triodopsis f. fosteri was originally described as a subspecies of *Mesodon appressus*. Anatomical studies revealed, however, that it belongs in the genus *Triodopsis*.

Triodopsis f. missouriensis of Illinois and Missouri is "small, rather smooth. . . . The parietal tooth is short and high. . . . The upper lip tooth is quite small, usually distinct, but sometimes disappearing. . . ." (Pilsbry, 1940: 833). None of these characters really differentiates *missouriensis* from "typical" *fosteri*, however. In size, *missouriensis* ranges from 14.3 to 15.8 mm, the typical form, 13.8–22.2 mm. Of the two specimens Pilsbry figured, one has a short parietal lamella, but the other has a long one. The former has an upper lip tooth, the latter lacks one. The range of *missouriensis* is peripheral to that of *f. fosteri*, but is not isolated from the latter. All in all, I cannot see any reason for separating *missouriensis* from *f. fosteri*. Therefore, I consider it synonymous with the latter.

Triodopsis fosteri hubrichti (F. C. Baker) Plate IV: 10, 11

Polygyra appressa var. *hubrichti* F. C. Baker, 1937, Nautilus 51: 23. Valmeyer, Monroe County, Illinois, in pink loess of Sangamon age. Paratypes ANSP 168631.

Definition. Triodopsis f. hubrichti is recognized here as proposed by its author.

Description and differential diagnosis. This subspecies was characterized by its author as follows: "Shell differing from typical *appressa* in its much greater size, more elevated spire, rounded aperture, and general gibbous form. The parietal lamella is long, curved, and extends to the umbilical region as in the typical form. Basal lower tooth of peristome usually well developed, but the upper denticle of race *fosteri* rarely developed. Sculpture of fine lines of growth. Diameter 25.5; height 14.5; Ap. [aperture] diam. 10.0; height 7.0 mm." Later, Baker writes (1937: 23), however, that "there is considerable variation in size among the 50 specimens of *hubrichti* from Valmeyer, about a dozen specimens ranging from 19 to 21 mm in diameter."

In contrast, Pilsbry states that "the race is distinguished only by its large size" (1940: 834). Having seen the type population, I agree with him completely.

Distribution and ecology. Triodopsis f. hubrichti has been found in pink loess of Sangamon age, at Valmeyer, Monroe County, Illinois. This is on the banks of the Mississippi River, where *f. fosteri* occurs today. It therefore appears possible that *f. hubrichti* occupied habitats similar to those occupied by *f. fosteri* today.

Systematics. Triodopsis f. hubrichti is very similar to *f. fosteri*. In addition, it is probably directly ancestral to the latter. On this basis, we could combine them in one taxon. But *f. hubrichti* is chronologically isolated from *f. fosteri*, and for this reason is accepted as a valid subspecies.

Summary. (1) *Triodopsis fosteri* is divided into two subspecies; *f. fosteri* and *f. hubrichti*. The former is a Recent form, the latter a fossil. *Triodopsis f. missouriensis* is a synonym of *f. fosteri*.

(2) *Triodopsis f. fosteri* is confined to the Mississippi Valley. It possibly shows habitat exclusion with *T. o. denotata*. *Triodopsis f. hubrichti* presumably occurred in similar habitats.

(3) The geographic variation is irregular.

Evolutionary relationships in the Triodopsis obstricta complex. Triodopsis obstricta and *T. fosteri* are certainly related, but we do not know anything about their evolutionary history. *Triodopsis o. obstricta* and *o. denotata* are assumed to have descended from a common ancestor. They were once isolated, and during isolation started to diverge. But recently they have re-established contact and started hybridizing; this may lead to their eventual merging. *Triodopsis f. hubrichti* lived during the Pleistocene epoch (Sangamon age), in the same geographical area and possibly in similar habitats as *f. fosteri*. We can assume that *f. hubrichti* developed into *f. fosteri* through slow transformation (phyletic speciation).

Subgenus *NEOHELIX*

Neohelix von Ihering, 1892, Zeitschr. Wiss. Zool. 54: 482.

Type. Helix albolabris Say, designated by Pilsbry, 1930, Proc. Acad. Nat. Sci. Philadelphia 82: 326.

This subgenus differs from *Xolotrema* only in having a larger shell and more capacious whorls, and in lacking an armature in the aperture. It thus could be easily lumped with *Xolotrema*. I retain the present system only because of the reasons stated before (p. 148).

The subgenus consists of one species complex: the *albolabris* complex.

The *albolabris* Complex

This complex contains four well-differentiated species: *albolabris, dentifera, multilineata*, and *divesta*. *Triodopsis albolabris* has three subspecies: *a. albolabris, a.*

alleni, and *a. major*; the three other species are monotypic.

Triodopsis albolabris (Say)
Triodopsis albolabris albolabris (Say)
Plate V: 3, 6, 11

Helix albolabris Say, 1817, Nicholson's Encyclopaedia, 1st American Edition, article "Conchology," species number 1, pl. 1, fig. 1. Neotype from Philadelphia, Pennsylvania, designated by Pilsbry, 1940: 837, fig. 849. Neotype ANSP 20199.

Mesodon albolabris var. *dentata* Tryon, 1867, Amer. J. Conch. 3: 39, pl. 7, fig. 6. Type not seen.

Helix albolabris var. *maritima* Pilsbry, 1890, Proc. Acad. Nat. Sci. Philadelphia 42: 283, 3 figs. Sand hills at Cape May, Cape May County, New Jersey. Not *Helix maritima* Draparnaud, 1805. Type not seen.

Polygyra albolabris var. *minor* Sterki, 1900, Ann. Rep. Ohio State Acad. Sci. 8: 31. "On the bank along the river," New Philadelphia, Tuscarawas County, Ohio. Type not seen.

Polygyra albolabris var. *goodrichi* G. H. Clapp, 1916, Ann. Carnegie Mus. 10: 539, pl. 32, figs. 16–18. Middle Sister Island, Essex County, Lake Erie, Ontario, Canada. Paratypes MCZ 139673.

Definition. Triodopsis a. albolabris is recognized here as defined by Pilsbry (1940). It contains those populations of the species which have mean values of 25–50 in character index. The method of computing character index is shown in Table XII. The subspecies slightly overlaps *T. a. alleni* in character index. The reason is explained in a later section.

Description. Shell width 20.2–35.6 mm; height 11.5–23.9 mm, height to width ratio 0.52–0.73; no umbilicus; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striation becoming more pronounced on subsequent whorls, about 2–3 striae per millimeter on last whorl; space between striae with a grid formed by intersecting spiral lines (40–50 per millimeter) and transverse wrinkles; grid delicate on younger whorls, becoming coarser toward aperture; deep spiral grooves on whorls built after an injury to shell; aperture round-oval; lip swelling from thin to very thick; lip teeth and parietal lamella usually absent; lower lip tooth replaced by a low, diffuse swelling; small parietal lamella occasionally present.

Distribution. Triodopsis a. albolabris ranges from Quebec to Michigan in the north, and to North Carolina and Mississippi in the south (Fig. 22). Its range is larger than that of any other taxon of *Triodopsis*.

The *measured material*, all MCZ, comes from the following localities: *Maine*: Aroostook, Penobscot, Oxford, Knox, and Cumberland counties. *Quebec*: Terrebone and Rouville counties. *Ontario*: Leeds, Hastings, Ontario, Peel, Wentworth, Essex, and Norfolk counties. *New Hampshire*: Carroll and Cheshire counties. *Vermont*: Orleans, Chittenden, and Windsor counties. *Massachusetts*: Middlesex, Plymouth, and Hampden counties. *Rhode Island*: Newport County. *Connecticut*: Middlesex and Fairfield counties. *New York*: Clinton, Washington, Columbia, Dutchess, Ulster, Herkimer, and Otsego counties. *Michigan*: Cheboygan, Alpena, Lelanau, Tuscola, Ionia, Washtenaw, and Kalamazoo counties. *New Jersey*: Morris County. *Pennsylvania*: Pike, Northampton, Sullivan, Clinton, McKean, Indiana, Philadelphia, Lancaster, Dauphin, Fulton, and Somerset counties. *Ohio*: Summit, Belmont, Lucas, Pickaway, Adams, and Hamilton counties. *Indiana*: La Porte, Bartholomew, and Dearborn counties. *Maryland*: Baltimore, Somerset, Prince Georges, and Alleghany counties. *Virginia*: York, Norfolk, Louisa, Prince Edward, Rockbridge, Roanoke, Wythe, and Lee counties. *West Virginia*: Jefferson, Grant, Randolph, Summers, and Raleigh counties. *North Carolina*: Tyrell, Craven, Columbus, Durham, Mitchell, Henderson, and Swain counties. *Kentucky*: Hart County. *Tennessee*: Polk County. A total of 86 samples, 1–21 specimens each, 468 specimens altogether.

Ecology. Triodopsis a. albolabris occurs in a variety of forest types, between sea level and 4000 feet elevation (Fig. 22; the latter record from Pilsbry, 1940: 836).

Table XII

Chart for Computing Character Index for *Triodopsis albolabris*. Method of Calculation: a Specimen with a Shell Width of 40.0 mm, a Height to Width Ratio of 0.75, Sculpture C, and Lower Lip Tooth Grade 4 Was Scored $(70 + 70 + 30 + 30)/2 = 100$, the Available Maximum Score.

Score	Width in mm	Height to width ratio	Sculpture	Lower lip tooth grade	
0	20.2–22.1	0.54–0.55	A	1	*a. alleni*
5	22.2–24.1	0.56–0.57			↑
10	24.2–25.3	0.58–0.59		2	↑
15	25.4–26.4	0.60	B		↑
20	26.5–27.6	0.61		3	↑
25	27.7–28.7	0.62			↑
30	28.8–29.9	0.63	C	4	*a. albolabris*
35	30.0–31.0	0.64			↓
40	31.1–32.2	0.65			↓
45	32.3–33.3	0.66			↓
50	33.4–34.5	0.67			↓
55	34.6–35.7	0.68			↓
60	35.8–37.7	0.69–0.70			↓
65	37.8–39.7	0.71–0.72			*a. major*
70	39.8–41.7	0.73–0.76			

According to collectors' rather sporadic remarks on the ecology, it occurs not only in wooded areas but also in thickets on sandy shores and in salt marshes. It has been found on offshore islands too. The great number of samples available indicates that the species is rather abundant in nature.

In the thickets growing on sandy beaches (both sea and fresh water) and "on the higher spots in salt marshes" (Pilsbry, 1940: 839) a characteristically small, high, and thin-shelled form is usually present. This appears to be an ecological form of polytopic distribution. This form was once called *T. a.* var. *maritima*, but recent authors consider it synonymous with *T. a. albolabris* (Pl. V, fig. 6). Another polytopic, ecological form is *T. a.* forma *goodrichi*, which has a pinkish shell. It is found on a few islands in Lake Erie, and on the shores of Lake Waccamaw, North Carolina, all presumably very moist places. This form also is considered synonymous with *T. a. albolabris*.

Variation. Aperture: The lip teeth are usually lacking. Rarely, however, a moderate to heavy swelling appears close to the columella, possibly replacing the lower tooth. A parietal lamella occurs sporadically in many populations.

Measured characters: Height of the shell is correlated with width; both characters show irregular geographic variation.

Systematics. The synonymy of *T. a. albolabris* has been summarized by Pilsbry (1940: 835), and is only recapitulated here. *Triodopsis a.* var. *maritima* and var. *goodrichi* are ecological forms, and var. *dentata* (Pl. V, fig. 2) is based on individual variation. *Polygyra a.* var. *minor* is a preoccupied name.

Triodopsis albolabris major (A. Binney) Plate V: 9, 10

Helix major A. Binney, 1837, Boston J. Nat. Hist. 1: 473, pl. 12. "Georgia, Alabama, and Florida." Neotype selected by Pilsbry, 1940: 844, fig. 489/1, "Georgia," ANSP 11212.

Definition. Triodopsis a. major is recognized here as defined by Pilsbry (1940). It contains those populations of the species of which the mean character index values range between 65 and 95. The method of computing character index is shown in Table XII.

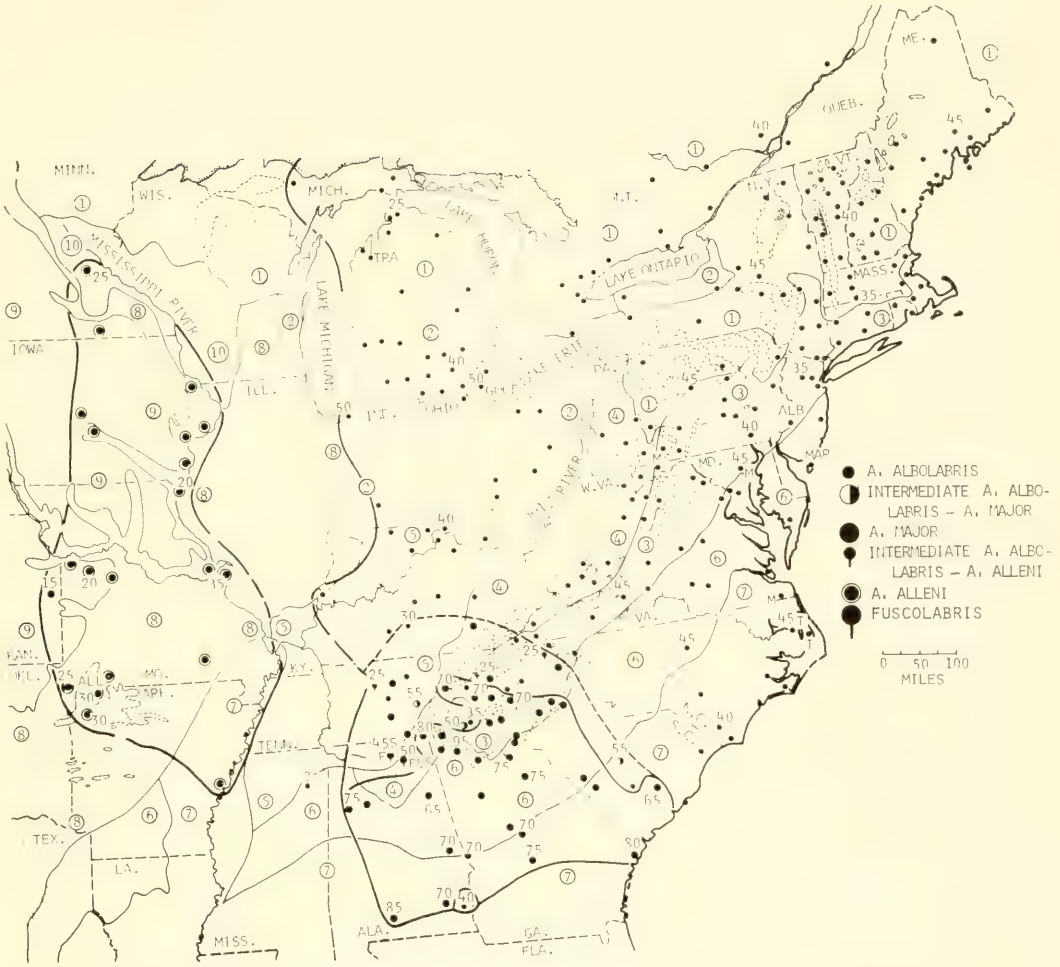

Figure 22. Distribution of *Triodopsis albolabris*. Thick, solid line surrounds the range of *a. albolabris, a. major* and *a. alleni*; thick, dashed line separates the zone of intergradation from the range of *a. albolabris*. F, occurrence of *fuscolabris*; M, *maritima*; T, *traversensis*; the latter two forms are considered synonymous with *a. albolabris*. ALB., type locality of *a. albolabris*; ALL., *a. alleni*; FUS., *fuscolabris*; GOOD., *goodrichi*, considered synonymous with *a. albolabris*; MAR., *maritima*; TRA., *traversensis*. Numbers without a circle are mean values of samples in character index; samples of *a. albolabris* range from 25 to 50; intermediate between *a. albolabris* and *a. major*, 50–55; *a. major*, 65–95; intermediate between *a. albolabris* and *a. alleni*, 25; *a. alleni*, 15–35; *fuscolabris*, considered intermediate between *a. alleni* and *a. major*, 45–50. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Description and differential diagnosis. Shell larger, higher, and more globose than that of *a. albolabris*; width 27.1–41.7 mm; height 18.8–30.5 mm, height to width ratio 0.62–0.74. Sculpture same as in *a. albolabris*, perhaps a little coarser. Lip swelling usually very thick; the swelling replacing the lower lip tooth is present in about two-thirds of the specimens; parietal lamella absent. In *a. albolabris*, the lip swelling is usually thinner, and the lip swelling and the parietal lamella are present occasionally.

Distribution. Triodopsis a. major is confined to a small area from North Carolina to Alabama (Fig. 22). A narrow zone of intergradation separates its range from that

of *T. a. albolabris*. The range roughly coincides with that of *T. f. alabamensis*, a not very closely related, congeneric species.

The *measured material*, all MCZ, comes from the following localities. *North Carolina*: Swain County. *South Carolina*: Berkeley County. *Tennessee*: Blount, Loudon, Cumberland, and Marion counties. *Georgia*: Whitefield, Hall, Clarke, Bibb, Chatham, Pulaski, and Muscogee counties. *Alabama*: Fayette, Calhoun, Lee, Barbour, Henry, and Conecuh counties. A total of 19 samples, 1–8 specimens each, 41 specimens altogether.

Ecology. *Triodopsis a. major* is common in oak-pine and southeastern evergreen forests, but also occurs in mixed and western mesophytic and oak-hickory forests. It ranges from sea level to over 3000 feet (Fig. 22).

Variation. Archer (1932), following Binney (1851: 97), speaks of the "narrow, thickened, rounded" peristome of *a. major* as a diagnostic feature. This holds true in some specimens, but many others have a relatively large aperture, almost like that in *a. albolabris*.

The *measured characters* are statistically correlated with each other and show irregular geographic variation. A few populations are morphologically intermediate between *a. major* and *a. albolabris*; these will be discussed in a later section.

Systematics. The conspecificity of *T. a. major* with *a. albolabris* is shown by the fact that they intergrade.

Triodopsis albolabris alleni (Wetherby, *In* Sampson)

Plate V: 4, 5

Mesodon albolabris Say var. *alleni* Wetherby, *In* Sampson, 1893, Ann. Rep. Geol. Surv. Arkansas for 1891, 2: 190. Eureka Springs, Carroll County, Arkansas. Paratype MCZ 79467.

Mesodon albolabris var. *minor* Wetherby, 1881, J. Cincinnati Soc. Nat. Hist. 4: 332. Eureka Springs, Carroll County, Arkansas. Not *Helix albolabris* var. *minor* Shuttleworth. Type not seen.

Definition. *Triodopsis a. alleni* is recognized here as defined by Pilsbry (1940). It contains those populations of the species which have mean values of 15–35 in character index. The method of computing character index is shown in Table XII. The subspecies slightly overlaps *T. a. albolabris* in character index, for reasons to be explained in a later section.

Description and differential diagnosis. Shell usually smaller and flatter than that of *a. albolabris*; width 23.3–30.1 mm; height 13.7–17.8 mm, height to width ratio 0.55–0.64; striated; intervals between striae shiny and smooth, or nearly so; grid, formed by intersecting spiral lines and transverse wrinkles, very faint; aperture oval, lip swelling thin, often with a very broad, low swelling near the columella; other characters as in *a. albolabris*.

Distribution. *Triodopsis a. alleni* is the western subspecies of *T. albolabris* (Fig. 22). It occurs west of the Mississippi River, from Minnesota to Iowa and south to Arkansas, or possibly to Texas (reported by Singley, 1893, quoted after Pilsbry, 1940: 841). Occasionally it is found on the eastern side of the river, as in Memphis, Shelby County, Tennessee.

The *measured material*, all MCZ, comes from the following localities: *Minnesota*: Hennepin County. *Illinois*: Hancock County. *Iowa*: Muscatine and Polk counties. *Missouri*: St. Louis, Johnson, and McDonald counties. *Kansas*: Miami County. *Arkansas*: Carroll and Washington counties. A total of 10 samples, 2–17 specimens each, 57 specimens altogether.

Ecology. *Triodopsis a. alleni* occurs predominantly in the oak-hickory forest region, but it penetrates the marginal zone of the prairies, and the maple-basswood and southeastern evergreen forests, also (Fig. 22). It ranges from 500 to slightly above 1500 feet elevation. It possibly shows ecological exclusion with *T. multilineata*.

Variation. The width and height of the shell are correlated. The width shows irregular geographic variation, the height to width ratio a gradual decrease from north

to south. This is one of the few clines in *Triodopsis.*

Systematics. The conspecificity of *T. a. alleni* with *a. albolabris* is shown by their intergradation. (See below.)

Populations intermediate between *Triodopsis a. albolabris, a. major,* and *a. alleni*

Three populations from Lexington County, South Carolina, and Bradley and Warren counties, Tennessee (seven specimens altogether), are intermediate between *T. a. albolabris* and *a. major.* Their mean values in character index are 50–55; in *a. albolabris* they are 25–50, in *a. major,* 65–95.

Two populations from Knox and Washington counties, Tennessee, and one from Davidson County, Tennessee (28 specimens altogether), resemble the trans-Mississippian subspecies, *a. alleni,* in having semismooth (B) sculpture (below) and a flattened shell, respectively. In other characters, they are like *a. albolabris.* The mean value of these populations in character index is 25; in *a. alleni* it is 15–35, in *a. albolabris* 25–50.

Two populations from Jackson and Madison counties, Alabama (13 specimens), are large and have a thick lip swelling like *a. major,* but at the same time the shells are flat and have a semismooth sculpture (B), in which characters they approach *a. alleni.* Their mean values in character index are 45 and 50. The Jackson County population is currently recognized as *T. a. fuscolabris*[1] (Pl. V, figs 7, 8); it is not so recognized in this paper, however (see below).

All these localities lie in the zone of intergradation between *T. a. albolabris* and *a. major* (Fig. 22). This makes sense as far as the *albolabris-major* intergrades are concerned, but it leaves the *albolabris-alleni* and *major-alleni* intergrades unexplained. Perhaps there was a time when *a. alleni* was continuous in distribution with *a. albolabris* and *a. major* through the Tennessee-Alabama region, and the intergrading populations are remnants of this lost connection. The observation that *T. neglecta* shows the same pattern of variation lends support to this hypothesis. In that species, too, the Tennessee-Alabama populations resemble the isolated western subspecies in certain characters.

The intergradation is probably due to simple variation. Hybridization is unlikely, because the range of the variation of the intergrading populations is not wider than that of other, presumably "pure," parental ones (for further discussion, see p. 236). One can treat these populations as intergrades, or they may be considered parts of *a. albolabris* or *a. major,* in which they belong geographically. I prefer the first solution, although it does not really matter what these populations are called. The important thing is that intergradation exists among the three subspecies.

As mentioned earlier, one of the populations that intergrades between *a. major* and *a. alleni* is recognized in the present literature as a separate subspecies, *T. a. fuscolabris.* It does not deserve this status, however. Not only does it lack morphological distinction; it also has no range of its own (Fig. 22).

Variation of the character index in Triodopsis albolabris. Four characters were utilized in making up the character index: size (width), height and sculpture of the shell, and degree of development of the lower lip tooth or the swelling that replaces it. The first two characters were measured, the third and fourth graded by comparison to standard specimens. In sculpture, three grades were distinguished. Shells of grade A are smooth and shiny between the striae, or almost so. In grade B, a faint grid is visible between the striae, formed by the superimposition of fine spiral lines on wavy, transverse wrinkles. In grade C, the grid is coarse. Four grades of development of the lower lip tooth were distinguished: (1) no tooth, (2) small

[1] Pilsbry described this population as *Polygyra albolabris fuscolabris,* from Woodville, Jackson County, Alabama (1903, Proc. Acad. Nat. Sci. Philadelphia 55: 200). Type ANSP 66304.

tooth, (3) medium, and (4) large. Each character was scored according to the chart shown in Table XII, and the scores summed to obtain the character index.

According to the geographic variation of the character index, three subdivisions can be recognized in the species. One has mean values of 15–35, and occurs west of the Mississippi (Fig. 22). Another has mean values of 25–50, and occupies most of the range east of the Mississippi. The third has mean values of 65–95, and occurs in the southeastern tip of the range. Thus the geographic variation of the character index clearly supports the view that three subspecies are recognizable within the species.

The reason that *a. albolabris* and *a. alleni* overlap in character index is that size is included; *a. albolabris* and *a. alleni* completely overlap in this character. Size was included for the better separation of *a. major*; as all three subspecies intergrade, it was desirable to cover all three with the same character index.

Evolutionary relationships. *T. a. albolabris* occupies a central position geographically; the other two subspecies are peripheral. This would seem to indicate that the former subspecies gave rise to the others. Morphologically, however, each of the three subspecies intergrades with the others, which supports the notion that all three evolved from a common, widespread ancestor by adapting to local selective forces.

Summary. (1) *Triodopsis albolabris* consists of three intergrading subspecies: *a. albolabris*, *a. major*, and *a. alleni*. The currently recognized subspecies *T. a. fuscolabris* is not worthy of taxonomic recognition.

(2) *Triodopsis a. alleni* is geographically isolated from *a. albolabris* and *a. major*; the latter two subspecies are separated from one another by a zone of intergradation.

(3) *Triodopsis a. alleni* occurs only in areas of moderate elevation. The other two subspecies have a broader ecological spectrum. *Triodopsis a. alleni* may be ecologically exclusive of *T. multilineata*.

(4) The geographic variation is irregular in all characters in all three subspecies, except the height to width ratio in *a. alleni*, which varies clinally.

(5) The three subspecies probably evolved independently of one another from a common ancestral stock.

Triodopsis dentifera (A. Binney)
Plate VI: 1–3

Helix dentifera A. Binney, 1837, Boston J. Nat. Hist. 1: 494, pl. 21. "In the state of Vermont, on the eastern slope of the Green Mountains." The possible type is a specimen in the MCZ collection, collected by A. Binney in "Vermont," labelled as "cotype (?)"; MCZ 152236, A. F. Gray Collection.

Mesodon dentiferus var. *major* Ancey, 1887, Conch. Exch. 1: 55. "Mountains of east Tennessee." Type not seen.

Definition. The taxon is used here as recognized in the current literature.

Description. Shell width 19.5–27.6 mm; height 10.6–15.6 mm, height to width ratio 0.52–0.57; no umbilicus; embryonic whorls 1.4–1.5, striated below suture; striation on subsequent whorls becoming more pronounced, 3–4 striae per millimeter on last whorl; intervals of striae with fine grid formed by intersecting spiral and transverse lines (about 40 spiral lines per millimeter); after breakage, deep spiral grooves appear; aperture oval, lip swelling strong and flat; no lip teeth; parietal lamella small.

Differential diagnosis. *Triodopsis dentifera* is very similar to *T. a. albolabris*, but its shell is smaller and flatter, and its lip swelling is heavier. In addition, it has a parietal lamella, whereas *a. albolabris* very rarely does.

Distribution. *Triodopsis dentifera* ranges from Quebec to Pennsylvania (Fig. 23). It also occurs farther south in the Tennessee-North Carolina region. Taft (1961) reports it from Hamilton County, Ohio. The latter areas seem to be isolated from the main part of the range. This pattern may imply that the species is in the withdrawal stage, but this is not certain. In Ohio, the species is adjacent to the related

species, *T. multilineata*. It appears that the two forms are replacing one another geographically.

The *measured material*, all MCZ, comes from the following localities: *Quebec*: Labelle County. *New Hampshire*: Cheshire and Grafton counties. *Vermont*: Lamoille and Windsor counties; one specimen (? cotype) from Vermont, without detailed locality. *New York*: Franklin County. *Pennsylvania*: Wayne and Allegheny counties. *North Carolina*: Watauga County. A total of 13 samples, 1–5 specimens each, 24 specimens altogether.

Ecology. Triodopsis dentifera is mainly found in the cool northeastern regions of the continent, covered by northern hardwood forests (Fig. 23). Only sporadic records are known from more southern regions, from oak-chestnut and mixed mesophytic forests. All localities lie above 500 feet elevation.

Variation. The variation of the species conforms to the pattern usually found in *Triodopsis*: width and height of shell are correlated, and the geographic variation of both characters is irregular. The variation is limited, as expected from the small size of the population.

Systematics. Triodopsis dentifera var. *major* was described from the mountains of eastern Tennessee. The type specimens are not known, but supposedly they were large (28 mm), dark colored shells, with deep spiral lines on the lower surface. Currently, *major* is considered synonymous with *dentifera*, for the reason that specimens of *dentifera* from Banner's Elk, Watauga County, North Carolina, are nearly as large (26.1–26.5 mm) as *major* was supposed to be, but otherwise are "normal" *dentifera*. I may add that the deep spiral lines, thought to be of diagnostic value, probably resulted from an injury, as these lines have been found in many injured specimens of the *albolabris*, *fosteri*, and *mullani* groups (Pl. V, fig. 11).

Summary. Triodopsis dentifera is a monotypic species. Its population is small, its variation narrow and irregular. Geographically, it replaces the related species *T. multilineata*.

Triodopsis multilineata (Say)

Plate VI: 4–7

Helix multilineata Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 150. Type unknown. Say gave "Illinois and Missouri" as the type locality; I restrict it to Hamilton, Hancock County, Illinois.

Polygyra multilineata subsp. *algonquinensis* Mason, 1906, Nautilus 19: 141. Marshy and boggy places around roots of willows; Algonquin, McHenry County, Illinois. Types MCZ 148145 and ANSP 91193.

Polygyra multilineata var. *chadwicki* Ferriss, 1907, Nautilus 21: 37. Banks of Kaw River, near Lawrence, Douglas County, Kansas. Paratypes MCZ 222099.

Polygyra multilineata var. *altonensis* F. C. Baker, 1920, Nautilus 34: 65. From loess, Alton, Madison County, Illinois. Type not seen.

Polygyra multilineata var. *wanlessi* F. C. Baker, 1928, Nautilus 41: 132. Peorian loess, east of Havana, Fulton County, Illinois. Type not seen.

Definition. Triodopsis multilineata as used here includes the currently recognized taxa *multilineata*, *m.* forma *algonquinensis*, and *m.* forma *chadwicki*.

Description. Shell width 16.2–28.1 mm; height 10.0–18.2 mm, height to width ratio 0.55–0.71; no umbilicus; embryonic whorls 1.4–1.5, smooth or finely striated below suture (20–25 striae per millimeter); striation becoming more pronounced on subsequent whorls, about two striae per millimeter on last whorl; third whorl with a grid formed by extremely delicate spiral and transverse lines; grid on subsequent whorls somewhat coarser, but still very fine (30 spiral lines per millimeter); shell banded with dark reddish brown bands, rarely uniformly dark reddish brown or horn colored; after breakage, deep spiral grooves may develop; aperture oval, without lip teeth; parietal lamella, or a callosity in its place, may be present.

Differential diagnosis. The thin lip and the banded shell readily distinguish this species from *T. albolabris* or *T. dentifera*.

Distribution. Triodopsis multilineata lives in the northern midwestern states,

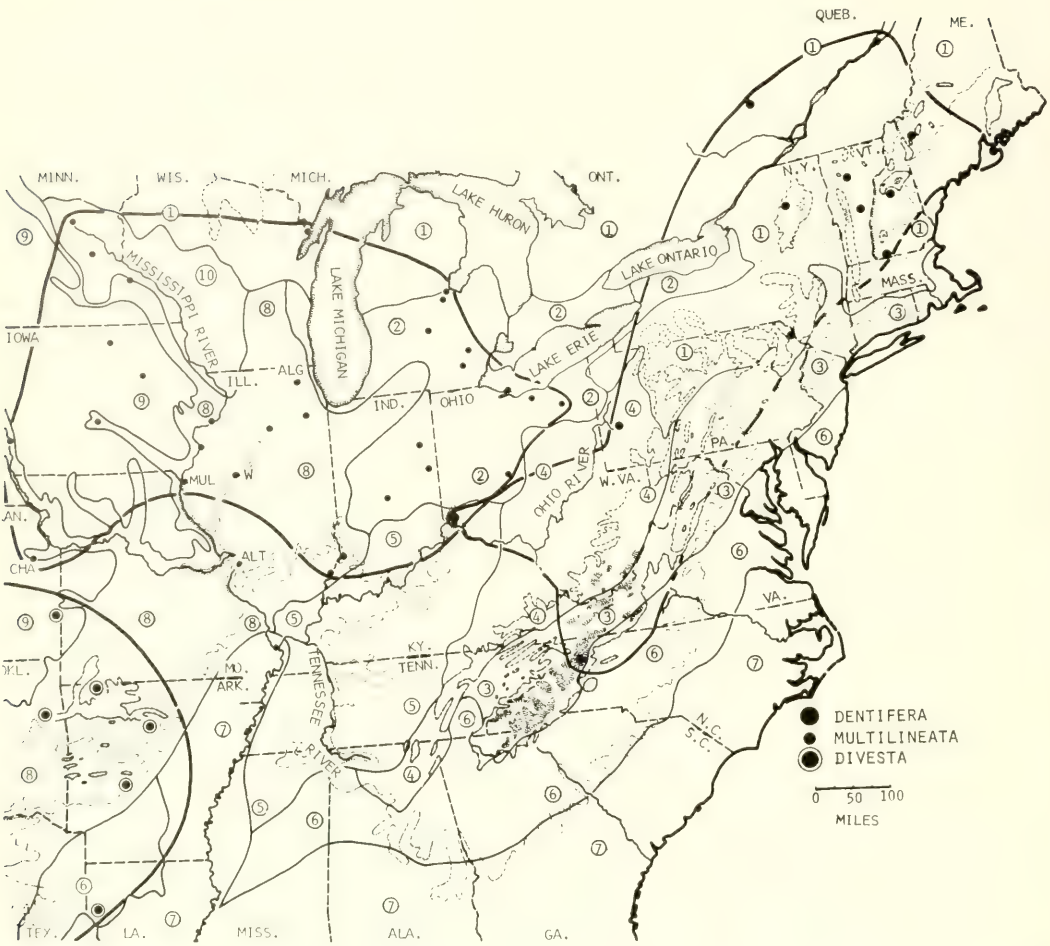

Figure 23. Distribution of *Triodopsis dentifera, multilineata,* and *divesta.* Thick, solid line surrounds the range of the three species. ALG., type locality of *algonquinensis;* ALT., *altonensis;* CHA., *chadwicki;* W., *wanlessi;* these forms are considered synonymous with *multilineata;* MUL., *multilineata.* Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

from Minnesota east to Michigan and Ohio and south to Kansas. Its range is adjacent to that of *T. dentifera* in the east and *T. divesta* in the west. The three forms apparently replace each other geographically (Fig. 23).

The *measured material* comes from the following localities: *Michigan*: Menominee, Huron, Saginaw, Oakland, Washtenaw, Clinton, Kent, and Calhoun counties. *Minnesota*: Stearns, Hennepin, and Goodhue counties. *Ohio*: Portage, Lorain, Ottawa, Franklin, and Hamilton counties. *Indiana*: Wells, Randolph, Marion, and Knox counties. *Illinois*: McHenry, Will, LaSalle, Mercer, Hancock, and Wabash counties. *Iowa*: Cerro Gordo, Black Hawk, Scott, Polk, and Pottawattamie counties. *Kansas*: Douglas County. A total of 32 samples, 2–25 specimens each, 230 specimens altogether.

Ecology. Triodopsis multilineata lives in oak-hickory, beech-maple, and maple-basswood forests (Fig. 23). A few localities also occur in northern hardwoods, in the western mesophytic forests, and in the

prairies. The prairie localities, however, may be the result of the inaccuracy of the map; its scale is too large to show very small patches of woods. All localities lie higher than 500 feet.

Various collectors have observed that the species prefers river banks and other moist places. It shares this preference with *T. a. alleni*, a sympatric form. Although I do not have personal experience with them, and the museum labels do not say it explicitly, I assume that the two species live in habitat exclusion—that is, in any given habitat either one of them may occur, but not the two together. This assumption is based on the behavior of numerous other sympatric species pairs of *Triodopsis*, such as *tridentata-juxtidens*, *juxtidens-fallax*, etc.

It may be that *T. multilineata* is also ecologically exclusive of *T. dentifera* and *T. divesta*. This could be inferred, at least, from the fact that it replaces these forms geographically (Fig. 23). Exclusion seems, however, less certain in these than in some other cases, since the three forms are separated from one another by gaps. Thus they are not in competition with one another, and without competition, one cannot assume exclusion.

Triodopsis multilineata has the interesting habit of gathering into groups for hibernation. Pilsbry (1940: 848) quotes Dr. Kirtland when writing: "At the approach of winter it [*T. multilineata*] retreats to the carex-tops, where several dozen may be found together in a torpid state, with the mouth of their shells closed with an epiphragm. . . . The numbers collected in these retreats are sometimes agglutinated into one mass." I observed hibernation in groups also in several species of the family Zonitidae.

Variation. Aperture: A small or medium large parietal lamella appears in specimens collected at Lawrence, Douglas County, Kansas. These specimens have been described as *T. m.* forma *chadwicki*. This is not justified in my opinion, however. For explanation, see systematics, below.

Color: The shell is usually ornamented with six to eight reddish brown bands on a light horn ground color. The bands may decrease in number until they entirely disappear, or may expand until the shell becomes entirely reddish brown. Banded and unicolored shells occur together in many populations. Despite this, however, the light shells were at one time recognized as var. *alba* or *albina*, the red ones as var. *rubra* or *rufa* or *unicolor*. Currently, these names are considered synonyms.

Among the *measured characters*, the width of the shell correlates with the height. Geographically, both width and the height to width ratio vary irregularly.

Systematics. Triodopsis m. forma *chadwicki* from Lawrence, Douglas County, Kansas, has been separated from the nominate form of *multilineata* because it has a parietal lamella and is uniformly dark reddish brown. These features occur, however, in several, widely separated populations of *multilineata*; also, not all specimens of *chadwicki* exhibit these features. In consequence, *chadwicki* is considered synonymous with *multilineata*.

Triodopsis m. forma *algonquinensis* (Pl. VI, fig. 4) from Algonquin, McHenry County, Illinois, is said to be an ecological form of the prairie region, which is characterized by its small body size, high spire, and dark color (Pilsbry, 1940: 850). My measurements on size and height do not show any significant difference between prairie and non-prairie populations, and the color variation, as shown above, is inconsequential. For these reasons, I propose to make *algonquinensis* synonymous with *multilineata*.

Following Shimek (1936) and Pilsbry (1940: 850), we may consider var. *wanlessi*, a loess form, identical with *algonquinensis*. "The fossil condition of *wanlessi* is about all that constantly separates them" (Pilsbry, *ibid.*). Since, as demonstrated above, *algonquinensis* is synonymous with *multilineata*, *wanlessi* is also a synonym.

Triodopsis m. var. *altonensis*, another

loess form, is claimed to be "larger . . . more gibbous . . . [and the] spire more depressed. . . ." than the typical form. Specimens as large and gibbous as *altonensis* occur, however, in several loess and Recent populations. Therefore, in agreement with Pilsbry (1940: 849), we may consider the name *altonensis* synonymous with *multilineata*.

Summary. (1) *Triodopsis multilineata* is a monotypic species; the forms *chadwicki* and *algonquinensis*, and varieties *wanlessi* and *altonensis* are individual or ecological variants of *multilineata*, and therefore synonymous with it.

(2) Geographically, *Triodopsis multilineata* replaces the related species *T. dentifera* and *T. divesta*. It prefers moist habitats. It hibernates in aggregates, a habit unique in *Triodopsis*.

(3) Another unique feature is its banded shell, the bands of which exhibit great variation in number and extent. All characters show irregular geographic variation.

Triodopsis divesta (Gould)
Plate VI: 8–10

Helix divesta Gould, 1851, *In*: A. Binney, The Terrestrial Air-breathing Mollusks of the United States 2: 358, and 3: 27, pl. XIIIa, fig. 2. Substitute name for *Helix abjecta* Gould. "Arkansas." Cotype MCZ 72831.

Helix abjecta Gould, 1848, Proc. Boston Soc. Nat. Hist. 3: 40. "South-western States." Not *Helix abjecta* Lowe, 1831.

Definition. The taxon *Triodopsis divesta* is recognized here as conventional.

Description. Shell width 16.9–19.5 mm; height 8.7–11.8 mm, height to width ratio 0.49–0.67; no umbilicus; embryonic whorls 1.3–1.5, finely striated (25 striae per millimeter); subsequent whorls with stronger, more widely spaced striae (3–4 per millimeter); intervals between striae with short and wavy transverse wrinkles, arranged loosely in spiral bands, which may be separated from one another by smooth bands; spiral lines also present, but so extremely fine that they are barely visible, even on fresh specimens; last whorl slightly angular at its periphery; aperture oval, with a lip swelling, but without lip teeth or parietal lamella.

Differential diagnosis. The shell of *Triodopsis divesta* is similar to that of *T. multilineata*, but is not banded; it has a distinctive microscopic sculpture.

Distribution. Triodopsis divesta occurs west of the Mississippi, from Kansas to Louisiana. It does not enter the Ozark Mountains proper, but stops at their foot (Fig. 23). Its range is adjacent to that of the related species *T. multilineata*, and the two species replace one another geographically.

The *measured material*, all MCZ, comes from the following localities. *Arkansas*: Van Buren, Carroll, and Garland counties; cotype from "Arkansas," without more detailed locality. *Kansas*: Bourbon County. *Oklahoma*: Cherokee County. *Louisiana*: De Soto County. A total of 7 samples, 1–13 specimens each, 24 specimens altogether.

Ecology. Triodopsis divesta lives in oak-hickory and southeastern evergreen forests; it also seems to penetrate the eastern margin of the prairie land; however, the localities from the prairie may be patches of woods too small to be shown on the map (Fig. 23). The species seems to prefer moderate elevations between 500 and 1500 feet. In this respect, it is similar to the allied species *T. multilineata* and *dentifera*.

It is possible that *T. divesta* shows habitat exclusion with *T. a. alleni*, which it completely overlaps. I do not have enough data to prove this, however.

Variation. The shell width is correlated with height; the width and the height to width ratio show irregular geographic variation.

Summary. Triodopsis divesta is a monotypic species. It shows geographic replacement with *T. multilineata*, and possibly habitat exclusion with *T. a. alleni*. Its geographic variation is irregular.

Evolutionary relationships among the members of the albolabris complex. Triodopsis albolabris displays a great overall

similarity to *dentifera*. On this basis, the two can be considered very closely related. It is not known, however, whether *dentifera* evolved from *albolabris*, or both developed from a common ancestor, because according to its distributional pattern, *dentifera* may equally well be a relic or a young species. Uncertainties beset the origin of *multilineata* and *divesta*, also. These species do not show clear affinities to one another, nor to *albolabris* or *dentifera*. We can only say that they probably evolved long ago from a *Neohelix* stock.

Subgenus *CRYPTOMASTIX*

Cryptomastix Pilsbry, 1939, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (1): XVII.

Type. Triodopsis mullani olneyae (Pilsbry) (a synonym of *T. m. mullani*, below), by original designation.

Cryptomastix differs anatomically from other subgenera of *Triodopsis* by having a flagellum and a twin pilaster in the genital apparatus. For this reason, and because it is widely isolated geographically from the other subgenera, it might be better considered a separate genus. I follow the current classification, however, and include it in *Triodopsis* because of considerations explained elsewhere (p. 148).

The subgenus consists of one species complex, the *mullani* complex, and a single isolated species, *germana*.

THE *MULLANI* COMPLEX

The *mullani* complex consists of three species: *mullani*, *sanburni*, and *devia*. *Triodopsis mullani* has two subspecies, *m. mullani* and *m. harfordiana*, that hybridize with each other. *Triodopsis sanburni* and *devia* are monotypic.

Triodopsis mullani (Bland and Cooper)
Triodopsis mullani mullani (Bland and Cooper)

Plate VII: 8–10, 12–14

Helix mullani Bland and Cooper, 1861, Ann. Lyc. Nat. Hist. New York 7: 363, pl. 4, figs. 16, 17. Near Coeur d'Alene Mission, Coeur d'Alene Mountains, Idaho. Topotype, labelled "probably one of original lot," ANSP 1901.

Triodopsis hemphilli W. G. Binney 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 38, pl. 1, fig. 17. Kingston, Shoshone County, Idaho. Type ANSP 11106.

Helix binominata Tryon, 1887, Man. Conch. 3: 146, pl. 38, figs. 98, 99. Substitute name for *Triodopsis hemphilli* W. G. Binney.

Polygyra (*Triodopsis*) *mullani* var. *olneyae* Pilsbry, 1891, Nautilus 5: 47. Spokane, Spokane County, Washington. Type ANSP 11112.

Triodopsis mullani Bland, var. *blandi* Hemphill, 1892, *In*: Binney, 4th Suppl., Bull. Mus. Comp. Zool. 22: 184. Post Falls, Kootenai County, Idaho. Type not seen.

Triodopsis populi Vanatta, 1924, Proc. Acad. Nat. Sci. Philadelphia 76: 26, figs. 3,4. Cottonwood Tree Canyon, on Snake River, 50 miles south of Lewiston, Nez Perce County, Idaho. Type ANSP 132939.

Polygyra mullani subsp. *hendersoni* Pilsbry, 1928, Proc. Acad. Nat. Sci. Philadelphia 80: 178, fig. 206. The Dalles, Wasco County, Oregon. Type ANSP 145479.

Helix (*Mesodon*) *mullani* Bland and Cooper, var. *oregonensis* Ancey, 1882, Le Naturaliste 2: 29. "Oregon oriental." Not *Helix oregonensis* Lea, 1839.

Triodopsis mullani subsp. *tuckeri* Pilsbry and Henderson, 1930, Nautilus 44: 121, pl. 5, figs. 8–10. On the Clearwater River near the junction of Fourth-of-July Creek, Idaho. Cotype ANSP 152334.

Triodopsis mullani subsp. *latilabris* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 863, fig. 500. Lower two or three miles of John Day Creek, Idaho. Type ANSP 175777.

Definition. Triodopsis m. mullani combines the forms classified by Pilsbry (1940) as *T. m. mullani, m. tuckeri, m. latilabris, m. olneyae, m. hemphilli, m. hendersoni, m. blandi*, and *T. populi*. It contains all those populations of the species which have mean values of 40–100 in character index. The method of computing character index is shown in Table XIII.

Description. Shell width 12.6–19.0 mm; height 6.2–10.6 mm, height to width ratio 0.48–0.60; umbilicus narrow to moderately wide, slightly or sometimes almost completely covered by reflected edge of lower lip; whorl number 5.1–5.9, whorl to width ratio 0.31–0.42; embryonic whorls 1.4–1.5,

Table XIII

Chart for Computing Character Index in *Triodopsis mullani*. Method of Calculation: a Specimen with a Shell Width of 18.6 mm, a Height of 10.2 mm, and a Whorl to Width Ratio of 0.32 was Scored 40 + 30 + 30 = 100, the Available Maximum Score.

Score	Width	Height	Whorl to width ratio	
0	8.6–9.7	4.0–4.9	0.50–0.53	*m. harfordiana*
5	9.8–10.9	5.0–5.9	0.47–0.49	
10	11.0–12.1	6.0–6.8	0.44–0.46	
15	12.2–13.2	6.9–7.7	0.41–0.43	
20	13.3–14.3	7.8–8.6	0.38–0.40	
25	14.4–15.4	8.7–9.6	0.35–0.37	
30	15.5–16.6	9.7–10.6	0.31–0.34	
35	16.7–17.8			
40	17.9–19.0			*m. mullani*

striated below suture; striae usually breaking into granules towards their ends; rest of embryonic whorls smooth; subsequent whorls covered by alternating weaker and stronger striae; intervals of striae with fine spiral lines, about 30 per millimeter; between these lines even finer transverse lines and on some specimens papillae also present; papillae reportedly with hairs, but I have not seen any; aperture triangular or trapezoid or oval; lip swelling thin to very thick, upper lip swelling sometimes bulging in region of upper lip tooth; lip teeth moderately large, small, or absent; lower lip tooth located close to right corner of aperture; parietal lamella very small to moderately large.

Distribution. Triodopsis m. mullani is confined to three more or less isolated areas between the Cascade Range and the Rocky Mountains (Fig. 24). One is at the eastern foothills of the Cascade Range, where the Columbia River crosses the range. Another lies in the region of the Spokane River, and the third in the region of the Snake River. Both of these lie on the western slopes of the Rockies. The low area between the Cascade Range and the Rockies remains unoccupied.

Triodopsis m. mullani is entirely allopatric with *T. devia*, and sympatric with *T. sanburni*, which are closely related species.

The *measured material*, all MCZ, comes from the following localities: *Montana*: Lincoln County. *Idaho*: Boundary, Shoshone, Kootenai, Latah, Washington, and Gem counties. *Washington*: Spokane County. *Oregon*: Umatilla and Wasco (2 samples) counties. A total of 11 samples, 1–11 specimens each, 37 specimens altogether.

Ecology. Triodopsis m. mullani occurs predominantly between 1500 and 6000 feet elevation. Extreme localities may occur, however, as low as 500 feet (Fig. 24). Pilsbry (1940: 861) reports that H. B. Baker found "typical *mullani*" at 5400–5600 feet, in larch-pine-hemlock forest, on schistose rocks, at rock slides, and springs around Twin Lakes, Stephens Peak, Shoshone County, Idaho.

The exact altitude of many localities is not known. The available data seem to indicate, however, that the variation of the aperture is correlated with elevation. See below.

Variation. In view of the fact that *Triodopsis m. mullani* is a relatively small population, its variation is unexpectedly great. This applies particularly to the aperture and the umbilicus.

Aperture: The lip swelling may be thick or thin, lip teeth moderate or small or entirely lacking, parietal lamella moderate or small. In all cases the extreme specimens intergrade. Considerable variation may occur within a single local population. Those populations with the thickest lip swelling and largest lip teeth seem to concentrate in the higher regions of the range, while those with a thinner lip swelling and small or obsolete teeth live in the lower regions. If this generalization is valid, *T. m. mullani* can be said to show the same trend as was observed in *T. tridentata, fallax*, and the *n. vulgata-fraudulenta* group, in which montane populations also have a stronger armature than do lowland populations.

The *sculpture* consists of striae, fine lines, and papillae. The striation is well

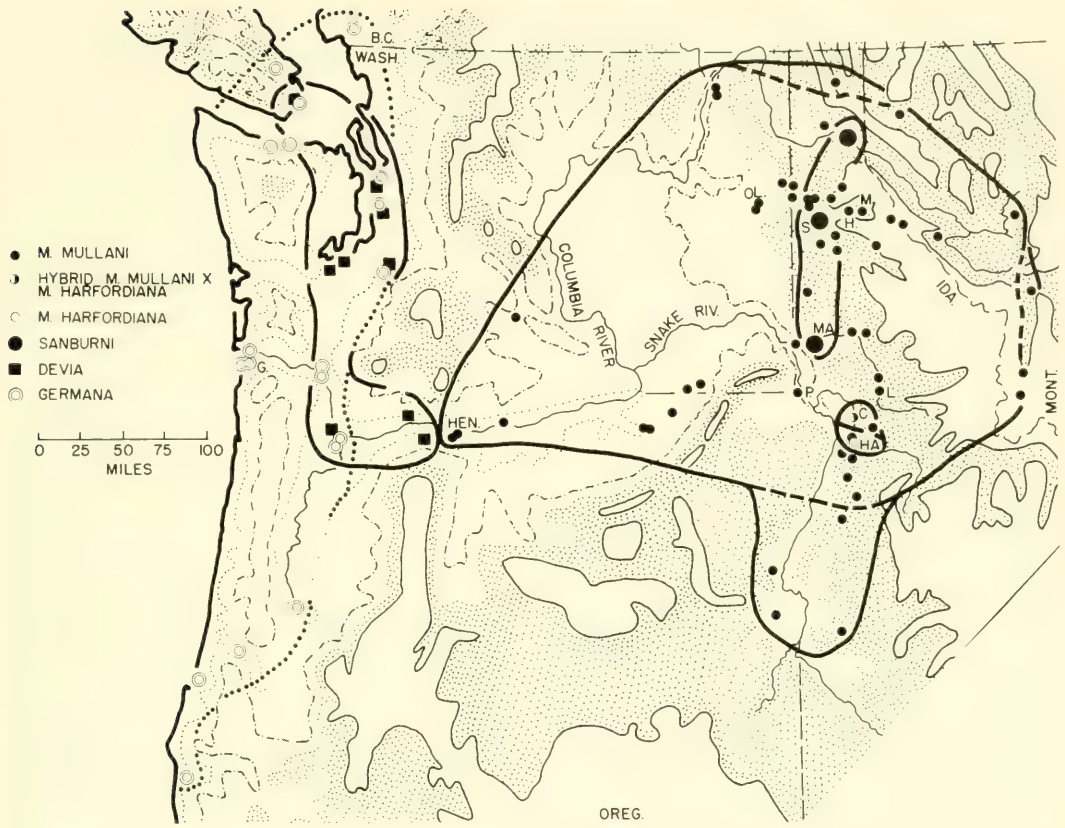

Figure 24. Distribution of *Triodopsis mullani, devia, sanburni,* and *germana.* Thick, solid lines surround the range of *m. mullani,* hybrid *m. mullani* × *m. harfordiana, m. harfordiana, sanburni,* and *devia;* thick, dashed line surrounds the range of *olneyae,* formerly recognized as a subspecies of *mullani,* here considered synonymous with *m. mullani;* dotted line surrounds the range of *germana.* G., type locality of *germana;* MA., *magnidentata,* considered synonymous with *sanburni;* S., *sanburni;* C., *clappi,* considered hybrid *m. mullani* × *m. harfordiana;* HA., *m. harfordiana;* H., *hemphilli;* HEN., *hendersoni;* L., *latilabris;* M., *m. mullani;* OL., *olneyae;* P., *populi;* the last six forms are all included in *m. mullani.* Elevation: . . . . . 656-foot contour line; . — . — . 1640–foot; area over 3281 feet is dotted; area over 6562 feet, blank, surrounded by thin, solid line. State boundaries are marked by thin, dashed lines.

developed on the upper side, where stronger and weaker striae alternate rather regularly (each strong stria is followed by two weak ones). On the lower side of the shell, the striation is nearly effaced. The intervals of the striae are covered by fine spiral lines, and the intervals of the latter are covered by even finer transverse lines. The spiral lines are pinched together at the papillae. The papillae are supposed to bear hairs, but I have not seen any with hairs. It is possible that in the shells examined they were worn off. Deep spiral lines also may be occasionally present. They may extend over the entire last whorl (or whorls), or may be restricted to a smaller or larger portion thereof, behind the aperture. These lines always follow a severe breakage in the shell and, therefore, are apparently the result of an injury to the mantle edge. This situation is similar to that found in *T. fosteri* and in the *T. albolabris* group.

The *umbilicus* may be very narrow to wide open. Considerable variation may occur within a single population. It is important to point out that there is no real corre-

lation between the variation of the umbilicus and the aperture. For instance, specimens with either a narrow or a wide umbilicus may have a weak aperture.

The *measured characters*, such as width, height, and whorl number, are statistically correlated with one another, and show irregular geographic variation.

The *character index* shows irregular geographic variation.

Systematics. Triodopsis m. mullani combines eight taxa ranked as separate subspecies or species in Pilsbry's classification (1940). These are: *Triodopsis m. mullani*, *m. olneyae*, *m. latilabris*, *m. tuckeri*, *m. blandi*, *m. hendersoni*, *m. hemphilli*, and *T. populi*. This large-scale lumping is necessitated by both morphological and distributional evidence. Because of the nature of the argument, I will not take up each taxon separately, but will discuss them together.

(1) Morphological evidence. In respect to the aperture and the umbilicus, the eight taxa form an uninterrupted morphological series. The aperture series starts with *hendersoni*, *blandi*, and *populi*, which totally lack lip teeth and have a thin lip swelling. It continues with *tuckeri* and *hemphilli*, with small lip teeth and a thin lip swelling; *olneyae*, having small to moderate lip teeth and a medium thick lip swelling. It ends with *latilabris* and *mullani*, which have small to moderate lip teeth and a very thick lip swelling. The umbilicus series starts with those specimens of *hemphilli* with a nearly imperforate shell. It continues with other specimens of *hemphilli*, and with those of *mullani*, *tuckeri*, and *hendersoni*, all of which have a narrow umbilicus. These are followed by *latilabris*, which has a narrow to medium wide umbilicus, and finally by *blandi*, *populi*, and *olneyae*, which have a medium wide umbilicus. In summary:

Aperture series: *hendersoni—blandi—populi—tuckeri—hemphilli—olneyae—latilabris—mullani.*

Umbilicus series: *hemphilli—mullani—tuckeri—hendersoni—latilabris—blandi—populi—olneyae.*

There are no convenient breaking points whereby the series could be subdivided. Nor does the aperture series coincide with the umbilicus series. Subdivisions based on the aperture are, therefore, in conflict with those based on the umbilicus. Such continuous and discordant variation should not be used for the separation of subspecies.

(2) Distributional evidence. (a) Populations with small or large lip teeth, or with a narrow or a wide umbilicus, do not form geographical races; instead, the aperture varies more or less in correlation with elevation, and the umbilicus varies irregularly. (b) One of the eight taxa in question, *olneyae*, completely overlaps *latilabris*, *mullani*, *tuckeri*, and *populi*, and partially overlaps *blandi*, *hemphilli*, and *hendersoni* (Fig. 24). Overlapping populations which have no morphological distinction should not be considered separate subspecies without further evidence. There is no such evidence in the present case.

Pilsbry himself was aware of this situation. On page 860 of his book (1940) he writes: "In fact, *mullani* and *hemphilli* seem to be merely the end forms in a continuous series, found in the same colonies, not really different races." On page 862: "In any large lot the variation from *mullani* to *hemphilli* is really continuous." On page 865: "In Idaho the line between *olneyae* and *hemphilli* is practically wiped out, since specimens referable to both or either, often occur in the same lots." On page 865: South of Stites, Idaho County, Idaho, ". . . the shells are small, rather delicate, thin, and strongly depressed as in *clappi*, but the callus in the basal lip is about as in the larger *olneyae*. . . ." On page 867: "In this area [Snake River Valley, around Weiser, Washington County, Idaho] it becomes a nice question where to draw the line between *hendersoni* and *clappi*." It is not at all clear to me why, in the face of such statements, he maintained the subspecific status of these forms, even adding new forms as late as 1940.

According to Pilsbry's classification, two more subspecies belong to *T. mullani*: *m. magnidentata* and *m. clappi*. In my opinion, *magnidentata* is identical with *T. sanburni*, and I therefore consider it a synonym of that species (p. 229). *Triodopsis m. clappi* is apparently a hybrid between *m. mullani* and *m. harfordiana*, and I therefore consider this name invalid.

Triodopsis mullani harfordiana W. G. Binney

Plate VII: 4–6

Triodopsis harfordiana W. G. Binney, 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 37. Salmon River, Idaho. Type MCZ 12674.

Helix salmonensis Tryon, September 2, 1887, Man. Conch., (2) 3: 146, pl. 38, figs. 96, 97. Salmon River, Idaho. Substitute name for *Triodopsis harfordiana* W. G. Binney 1886. Type ANSP 11116.

Helix commutanda Ancey, December 1887, Conch. Exch. 2: 79. Substitute name for *Triodopsis harfordiana* W. G. Binney 1886.

Definition. Triodopsis m. harfordiana corresponds to *T. harfordiana* of Pilsbry (1940: 869). It contains those populations of the species which have mean values of 0–5 in character index. The method of computing character index is shown in Table XIII (p. 224).

Description. Shell width 8.6–10.1 mm; height 4.0–4.8 mm, height to width ratio 0.43–0.51; umbilicus wide, cylindrical; number of whorls 4.6–5.1, whorl to width ratio 0.47–0.53; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striae closely spaced on subsequent whorls, about 9–10 per millimeter; all striae about equally strong, and equally well developed on upper and lower surfaces of shell; in spaces between striae fine spiral and transverse lines and hair-bearing papillae may be present (contrary to Pilsbry's claim, 1940: 870); last whorl sometimes slightly angular at its periphery; aperture low trapezoid; lip swelling moderately thick; upper lip tooth moderately large, lower long, bladelike; parietal lamella straight and long, pointing above or at upper lip tooth.

Differential diagnosis. Triodopsis m. harfordiana differs from *m. mullani* in its smaller, flatter, and more evenly striated shell, more closely arranged hairs, and wider and more cylindrical umbilicus.

Distribution and ecology. Triodopsis m. harfordiana is confined to the valley of the Salmon River, a tributary of the Snake River (Fig. 24). The Salmon River cuts deep into the mountains; the *m. harfordiana* population therefore seems to be well isolated from the rest of the species. The isolation cannot be a permanent one, however, since invasions have occurred repeatedly (see discussion of hybrids).

The *measured material* (5 samples, 1–3 specimens each, 9 specimens altogether, all MCZ) comes from the Salmon River Valley, probably north of Lucile, Idaho County, Idaho; exact localities are not given. Some samples were collected on the river banks. The elevation of the area is about 2000–2500 feet.

Variation. Because the total population is small and the area restricted, the variation of *Triodopsis m. harfordiana* is very narrow. A positive correlation is evident, however, between width, height, and whorl number.

Systematics. Triodopsis m. harfordiana is considered conspecific with *m. mullani* because they hybridize. The occurrence of hybridization is indicated by morphological studies, and is supported by the pattern of distribution.

The nomenclature of *T. m. harfordiana* has had a rather confusing history, which was well summarized by Pilsbry (1940: 870). When W. G. Binney first mentioned the name *Triodopsis harfordiana*, in 1878, he gave J. G. Cooper as the author and, like Cooper, included in the species the Californian polygyrid *Daedalochila harfordiana*. Having noticed his error, in 1886 Binney gave a new description and a figure for *Triodopsis harfordiana*, excluding *Daedalochila harfordiana*, and omitting Cooper as author. In 1887, both Tryon and Ancey renamed *T. harfordiana*, because they ar-

gued that the name was a homonym of *Helix harfordiana*. Tryon's name, *salmonensis*, was used subsequently in the literature until 1923, when the Nomenclature Committee of the American Malacological Union decided to drop it in favor of Binney's *harfordiana*. The Committee felt that Binney in 1886 had described a "new" species; therefore his name was valid. This usage has been accepted ever since.

Hybrid populations between *Triodopsis m. mullani* and *m. harfordiana*

Plate VII: 7, 11

In a sample from Salmon River, Idaho County, Idaho, "good" *m. mullani* and intermediates between *m. mullani* and *m. harfordiana* occur together. The mean value of this sample in character index is 35, that of *m. mullani* is 40–100, of *m. harfordiana*, 0–5. Another sample, collected in the same area, contains one intermediate specimen and two "good" *m. harfordiana*; the mean value of this sample is 15. A third sample, also from the Salmon River, consists exclusively of intermediate specimens; the mean value is 35. A total of 3 samples, 3–6 specimens each, 12 specimens altogether.

The first two samples are more variable than any other sample of the species, which indicates that they are of hybrid origin. Their geographical distribution is consistent with this statement: they occur in areas where both *m. mullani* and *m. harfordiana* live in proximity (Fig. 24). It appears probable that after an earlier period of isolation, during which *m. mullani* and *m. harfordiana* differentiated into separate subspecies, *m. mullani* secondarily "invaded" the area of *m. harfordiana*. Because of a lack of internal isolating mechanisms, this resulted in hybridization between the two populations.

The third sample shows only normal variation. But it also is considered hybrid, because it is very similar to the putative hybrids, and occurs in the same area.

The intergradation between *mullani* and *harfordiana* (old usage) indicates that these taxa are, in reality, conspecific. Workers who treated them as separate species overlooked the intergradation. The correct names for *mullani* and *harfordiana* are, accordingly, *m. mullani* and *m. harfordiana*. The sample that contains exclusively intermediate specimens was described as *T. m. clappi* (Hemphill, 1897, Nautilus 11: 74; type ANSP 71479). This name is to be considered invalid.

Evolutionary relationships. Triodopsis m. harfordiana can be considered a geographic isolate of *m. mullani*. As may be recalled, *m. mullani* occupies the whole valley of the Snake River, whereas *m. harfordiana* is confined to the valley of the Salmon River, a small tributary thereof. On this basis, it appears likely that *m. harfordiana* developed from *m. mullani*.

Triodopsis m. mullani lives in a mountainous area. The higher mountain ridges are likely to impede gene flow between the various parts of the population or even between neighboring demes. Thus, the Spokane River population is pretty well isolated from the population living in the upper valley of the Snake River (Fig. 24). Not ridges, but the wide open basin of the Columbia River separates the Cascade Range and the Rocky Mountain populations. These groups may in time become separate subspecies or even species.

Summary. (1) *Triodopsis mullani* has two subspecies: *m. mullani* and *m. harfordiana*. *Triodopsis m. mullani* combines the former *m. mullani*, *m. latilabris*, *m. tuckeri*, *m. olneyae*, *m. hemphilli*, *m. hendersoni*, *m. blandi* and *T. populi*. *Triodopsis m. harfordiana* corresponds to the former *T. harfordiana*. The former *T. m. magnidentata* is excluded from the species, and is attached to *T. sanburni* as a synonym. The former *T. m. clappi* is considered an invalid name, since it was given to a hybrid population.

(2) The two recognized subspecies are quite distinct morphologically. Their con-

specificity is shown by the fact that they hybridize.

(3) *Triodopsis m. mullani* occurs in three isolated areas in the basin of the Columbia River. *Triodopsis m. harfordiana* is confined to a small tributary of this river. The hybrids occur near *m. harfordiana.*

(4) *Triodopsis m. mullani* occurs predominantly between 1500 and 6000 feet; rarely, however, it may occur as low as 500 feet. *Triodopsis m. harfordiana* and the hybrids occur around 2000–2500 feet.

(5) The variation of *T. m. mullani* is greater than would be expected from its relatively small population and the relatively limited area it occupies. The variation of the aperture may be correlated with the elevation; other characters show irregular geographic variation. The measured characters are statistically correlated. The variation of *T. m. harfordiana* is very narrow. The putative hybrid populations are more variable than either of the parents.

Triodopsis sanburni W. G. Binney
Plate VII: 15–18

Triodopsis sanburni W. G. Binney, 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 37, pl. 1, fig. 9; pl. 3, fig. 3. Kingston, Shoshone County, Idaho. Paratypes MCZ 53463 and 133029.

Triodopsis mullani subsp. *magnidentata* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 862, fig. 499 f, f'. Mission Creek, 7 or 8 miles above Jaques Spur, Nez Perce County, Idaho. Type ANSP 171243.

Definition. Triodopsis sanburni combines the taxa formerly known as *T. sanburni* and *T. mullani magnidentata.*

Description. Shell width 10.1–11.3 mm; height 5.8–7.0 mm, height to width ratio 0.54–0.62; umbilicus half covered by reflected edge of aperture; number of whorls 5.5–5.8, whorl to width ratio 0.50–0.54; embryonic whorls 1.4–1.5, coarsely striated below suture; striae broken into granules towards their ends; embryonic shell smooth elsewhere; the following one and one-half whorls with fine transverse striae and papillae (in contrast to Pilsbry, 1940: 859, who claims that "no hairs and no regularly arranged points [papillae] such as appear in . . . *T. mullani*" are present); subsequent whorls with 2–3 striae per millimeter on their upper side, striae alternately weak and strong; underside of shell with weak striae only; some shells possibly with very fine spiral and transverse lines as in *T. mullani* and *T. devia*, but this cannot be seen clearly because shells are worn; aperture low square, with a moderate or very thick lip swelling and moderately large lip teeth; upper lip tooth marginal or somewhat receding, lower lip tooth marginal or a bit bulging out of aperture; parietal lamella large and straight, sometimes slightly concave.

Differential diagnosis. Triodopsis sanburni differs from *T. m. mullani* in its smaller dimensions, larger lip teeth and parietal lamella, and tighter coiling of the shell. Also, its umbilicus is always half covered, whereas that of *m. mullani* is often open.

Distribution and ecology. Triodopsis sanburni occupies a restricted area in northern Idaho (Fig. 24). It is completely overlapped by *T. m. mullani*, a closely related form. This is rather rare in *Triodopsis* and, generally speaking, in any animal group, since closely related forms are expected to occur allopatrically, in accordance with the theory of geographic speciation. The *T. n. vulgata-fraudulenta* and *a. albolabris-dentifera* pairs can be cited as the only other exceptions to this rule in *Triodopsis.*

The *measured material* comes from the following localities: *Idaho*: Shoshone and Kootenai counties (2 samples each, MCZ); Nez Perce County (ANSP). A total of 5 samples, 1–5 specimens each, 12 specimens altogether.

All specimens were found in valleys or near lakes, between 1600 and 3500 feet elevation.

Variation. Triodopsis sanburni has rather a narrow range of variation, probably because of its small populations and limited

TABLE XIV

MEASUREMENTS OF REPRESENTATIVE SAMPLES OF *TRIODOPSIS M. MULLANI*, *T. M. MAGNIDENTATA*, AND *T. SANBURNI*. THE ARROWS POINT TOWARD THE TAXON TO WHICH *MAGNIDENTATA* BEARS THE GREATER SIMILARITY. ON THIS BASIS, *M. MAGNIDENTATA* IS CONSIDERED SYNONYMOUS WITH *SANBURNI*.

NAME	REMARK	LOCALITY	NO. OF SPECIMENS	MEAN OF: WIDTH IN MM	MEAN OF: HEIGHT TO WIDTH RATIO	MEAN OF: WHORL TO WIDTH RATIO
m. mullani	average	Spokane County, Washington	11	15.3	0.53	0.35
m. mullani	smallest, with highest whorl to width ratio	Kootenai County, Idaho	3	12.7	0.50	0.39
m. magnidentata		Nez Perce County, Idaho	1	11.0	0.51	0.48
sanburni		Kootenai County, Idaho	4	10.5	0.58	0.51
sanburni		Kootenai County, Idaho	5	10.8	0.56	0.52

area of distribution. A correlation between shell width, height, and whorl number can be observed, as is customary in *Triodopsis*. Geographically, all characters vary irregularly.

Systematics. The form described as *Triodopsis mullani magnidentata* is said to differ from *T. sanburni* "by the strongly depressed shape and the fewer, less closely coiled whorls" (Pilsbry, 1940: 862). My measurements (Table XIV) show, however, that *magnidentata* is nearly identical with *sanburni* in these supposedly diagnostic features. For this reason, I consider *magnidentata* synonymous with *sanburni*.

Evolutionary relationships. Judging from the fact that *T. sanburni* is found in a much smaller area than the closely related *m. mullani*, we may infer that it has evolved from the latter. The fact that it is completely overlapped by *m. mullani* could be taken as an indication that it evolved through sympatric speciation; because, if it had evolved through geographic speciation, one would expect it to be allopatric to *m. mullani*. It is easy to see, however, that in a mountainous area like that of *sanburni*, local populations can become isolated and thus may speciate even in the center of the range. Secondary overlap could easily occur afterwards. Thus this case can be satisfactorily explained in terms of geographic speciation.

It is also interesting to note that while *sanburni* has achieved reproductive isolation from *m. mullani*, another descendant of the latter, *m. harfordiana*, has failed to do so, despite the fact that morphologically it is at least as dissimilar from *m. mullani* as is *sanburni*. Thus it appears that in *m. harfordiana* the development of reproductive isolating mechanisms has lagged behind that of morphological isolation, whereas in *sanburni* the two processes were concomitant. Similar cases are cited elsewhere in this paper (p. 236).

Summary. *Triodopsis sanburni* is a monotypic species; it includes the former *T. mullani magnidentata* as a synonym. It has a small population, a restricted area of distribution, and a narrow range of variation. It probably evolved from the ancestral *mullani* stock, through geographic isolation.

Triodopsis devia (Gould)
Plate VII: 1–3

Helix devia Gould, 1846, Proc. Boston Soc. Nat. Hist. 2: 165. Puget Sound, Washington. Type not seen.

Helix baskervillei Pfeiffer, 1850, Proc. Zool. Soc. London for 1849, 17: 130. Vancouver Island. Type not seen.

Definition. The name *devia* is used here in the conventional sense, including *baskervillei.*

Description. Shell width 19.4–26.0 mm; height 12.0–17.4 mm, height to width ratio 0.60–0.67; umbilicus almost entirely covered by reflected edge of peristome; number of whorls about 5–6; embryonic whorls 1.4–1.5, coarsely striated below suture; striae broken up into granules towards their ends; subsequent one and a half whorls with papillae and extremely fine striae, perhaps with hairs on papillae; remaining whorls striated, one strong and two or three weak striae per millimeter; strong striae rapidly subsiding towards periphery of whorl; intervals between striae with extremely fine spiral and transverse wrinkles, about 30 spiral wrinkles per millimeter; deep spiral grooves appearing after breakage; aperture square, lip swelling thick, marginal; lower lip tooth broad and very low, located near columella; upper lip tooth absent; parietal lamella short, low, sometimes merely a callosity.

Differential diagnosis. Triodopsis devia is distinguished from the related species *m. mullani* and *sanburni* by its greater size and by the fact that its lower lip tooth is located nearer to the columella than that of *m. mullani* and *sanburni.*

Distribution and ecology. Triodopsis devia occurs in the coastal area from Vancouver Island to Oregon (Fig. 24). Its area is separated from that of the related species *mullani* by the Cascade Range. At the point, however, where the Columbia River breaks through the mountains, the two species are in contact. *Triodopsis devia* is restricted to low elevations, below 600 feet. Pilsbry mentions (1940: 858) that it was found in damp places.

The *measured material*, all MCZ, comes from the following localities. *Washington*: King (2 samples), Pierce, Thurston, and Clark counties. *Oregon*: Hood River County. A total of 6 samples, 1–2 specimens each, 8 specimens altogether.

Variation. No appreciable variation can be seen on the available, very limited material.

Evolutionary relationships. Triodopsis devia is probably derived from *m. mullani*, which seems to be the central stock of the *mullani* complex. It is less likely that *devia* would be the ancestral form, because its range is peripheral to that of *m. mullani.* Furthermore, *m. mullani* shows greater affinity than *devia* does to *sanburni* and *m. harfordiana*, the other members of the complex.

Summary. Triodopsis devia is a monotypic species, of limited distribution and variation. It prefers low elevations. It is probably a descendant of *m. mullani.*

Triodopsis germana (Gould)
Plate VII: 19–23

Helix germana Gould, *In*: Binney, 1851, the Terrestrial Airbreathing Mollusks of the United States 2: 156, pl. 40a, fig. 3. Gould gave "Oregon" as type locality. Pilsbry (1940: 974) restricted the type locality to Astoria, Clatsop County, Oregon. Type not seen.

Polygyra germana vancouverinsulae Pilsbry and Cooke, 1922, Nautilus 36: 38. Cameron Lake, under dead bark on the ground, in open pine forest, Vancouver Island, British Columbia. Type ANSP 44538.

Definition. Triodopsis germana combines two taxa formerly considered separate subspecies: *g. germana and g. vancouverinsulae.*

Description. Shell width 6.6–6.8 mm; height 4.1–5.7 mm, height to width ratio 0.58–0.70; number of whorls 4.9–5.5, whorl to width ratio 0.62–0.78; umbilicus closed or almost closed; embryonic whorls 1.4–1.5, with papillae below suture; papillae arranged in transverse rows; subsequent whorls with fine transverse striae and papillae, rows of papillae becoming oblique; each papilla bearing a long, thick hair; last whorl slightly angular at its periphery; aperture oval or slightly auriculate; lip swelling moderately thick except near junction of upper lip with shell, where obsolete; no

lip teeth; parietal lamella long and straight, very low, higher only at its upper end.

Differential diagnosis. Triodopsis germana is different from all other species of *Triodopsis* by virtue of its small and hairy shell, almost closed umbilicus, long and low parietal lamella, and absence of lip teeth. It looks very much like a *Stenotrema*. Only its anatomy shows that it belongs in *Triodopsis*.

Distribution and ecology. Triodopsis germana is known from the coastal region and the lower valleys of Oregon, Washington, and British Columbia. It never occurs higher than 500 feet (Fig. 24). It has been reported from open pine forests on Vancouver Island.

Variation. The whorl to width ratio tends to decrease from the north to the south. This may be a true clinal variation, but one cannot eliminate the possibility that chance alone causes it, since only a few samples are known. The width and height to width ratio show slight and irregular geographic variation.

Systematics. Triodopsis g. vancouverinsulae was subspecifically separated from *g. germana* because it is "in the average smaller, distinctly perforate, with a shallower furrow behind the outer and basal margins of the lip, a less prominent crest preceding it. Sculpture as in *germana* [*g. germana*], but the hairs generally lost in the adult stage" (Pilsbry, 1940: 874). These distinctions are valid if only the type populations are considered. When more samples are studied, it becomes evident that they do not hold true. The size of the shell, the furrow behind the aperture, and the crest that precedes it may be nearly equal in the two alleged subspecies. According to the figures by Pilsbry (1940: figs. 505 C and D) the hairs are much scarcer in *g. vancouverinsulae* than in *g. germana*. But in this character, too, the two forms intergrade. Consequently, I propose to consider *g. vancouverinsulae* synonymous with *g. germana*.

The *evolutionary relationships* of *Triodopsis germana* are completely obscure. It is so different in shell characters from all other species of the genus that not even an approximate guess can be made about its evolutionary relationships with them. It is included in the subgenus because of its anatomy and distribution.

Summary. Triodopsis germana is a monotypic species. The former *T. g. vancouverinsulae* can no longer be recognized as a separate subspecies; instead, it must be considered synonymous with *germana*. The species occurs in the northern Pacific coastal region, always at low elevations. It probably shows clinal variation in whorl to width ratio, but in other characters it varies irregularly. Its evolutionary relationships with other species of the genus are obscure.

Summary of Systematic Treatment

In conclusion, let us compare the classification proposed in this paper with that current in the literature (Table XV). In contrast to the 19 monotypic and 12 polytypic species with 41 subspecies of the current system, the new classification recognizes only 13 monotypic and 9 polytypic species with 21 subspecies. Thus, the number of taxa is reduced from a total of 60 to 34, that of the species from 31 to 22, notwithstanding the fact that some old taxa have been split, and a new subspecies described.

The reduction of the number of taxa was not the main goal of the study. It is rather the by-product of the use of quantitative methods and the consistent application of the biological species concept of the group studied. These led to the synonymization of poorly distinguished taxa with recognized species or subspecies, and to the combination of intergrading taxa (primary or secondary) in one species. Thus arose a greatly simplified system.

For assigning taxonomic rank to closely related, allopatric populations, the "yardstick method" has been recommended (Mayr, Linsley, and Usinger, 1953: 103). In principle, the method is correct, but

there seem to be so many exceptions to it in *Triodopsis* that its use was abandoned. For example, *Triodopsis f. fallax* looks at least as different from *T. f. alabamensis* as *T. tridentata* does from *T. c. complanata*, and yet the former two taxa hybridize, the latter two are reproductively isolated. Similarly, *T. j. juxtidens* and *j. stenomphala*, *T. c. copei* and *c. cragini*, *T. o. obstricta* and *o. denotata*, and *T. m. mullani* and *m. harfordiana* are morphologically as different from one another as *T. fraudulenta* or *T. pendula* is from *T. n. vulgata*, or *T. a. albolabris* from *T. dentifera*, or *T. m. mullani* from *T. sanburni*, yet the former pairs interbreed, the latter do not. Instead of using the degree of morphological similarity as a yardstick, therefore, each case was judged on whatever evidence was available.

EVOLUTIONARY PROBLEMS

The term "evolutionary" is used here in a broad sense, including aspects of evolutionary biology as diverse as speciation, isolating mechanisms, hybridization, and adaptiveness and irregularity of geographic variation.

Speciation

The theory of geographic speciation is so firmly established that one can take it for granted that it also applies to *Triodopsis*. Nevertheless, it seemed worthwhile to make a brief study of the speciation in *Triodopsis*, which belongs to a lower and less studied group than *Drosophila* or the birds.

The study consisted of preparing hypothetical models, one for geographical speciation, another for sympatric speciation, and comparing the observed situation with these models. If speciation took place through geographic isolation, we should find the most closely related forms, that is, the incipient or very recently developed species, occurring allopatrically. If speciation took place according to the model of sympatric speciation, we should find the most closely related forms occurring sympatrically. The distribution of the more distantly related forms is less illuminating, since during their longer existence their range of distribution may have changed profoundly. In addition, the evolutionary relationships are often obscure among these older forms. For these reasons, the distribution of the distantly related forms was not considered.

Accordingly, the most closely related taxa were combined into pairs, and the pairs were classified according to distribution (Table XVI and Fig. 25). In 8 of the 20 cases (40%), the members of the pair are spatially separated from one another, in 9 cases (54%) they are in contact or slightly overlap, and in 3 cases (6%) they extensively overlap.

These data illustrate that speciation in *Triodopsis* was predominantly geographic. The first group (40%) is clearly indicative of speciation through geographic isolation. The second group (54%) also indicates geographic speciation, since it is much easier to assume that the narrow overlap is secondary than it is to assume that both overlapping taxa originated in the overlap zone, through sympatric speciation, and are now moving away from one another. The third group (6%) could possibly be interpreted as indicative of sympatric speciation. But the *T. fraudulenta-T. n. vulgata* and *T. m. mullani-T. sanburni* pairs occur in mountainous areas where spatial isolation is easy to achieve, and thus it seems very likely that spatial isolation played a role in the formation of these taxa. Only in the case of the *T. a. albolabris-T. dentifera* pair is the role of spatial isolation not evident. This is not to say that *dentifera* evolved from or gave rise to *a. albolabris* through sympatric speciation. It merely points out that the distribution of these taxa does not conform to the pattern generally considered "normal." One possible reason for this is that the deceiving morphological similarity between the two taxa actually conceals a more distant evolutionary relationship.

TABLE XV

COMPARISON OF THE CURRENTLY USED CLASSIFICATION WITH THAT PROPOSED IN THIS PAPER. THE FORMER IS A COMPILATION FROM THE WORKS OF PILSBRY (1940), HUBRICHT (1950b, 1952a, 1952b, 1954, 1958), AND LUTZ (1950).

CURRENT CLASSIFICATION		CLASSIFICATION ADOPTED IN THIS PAPER	
SPECIES	SUBSPECIES	SUBSPECIES	SPECIES
	Subgenus: *Triodopsis*	Subgenus: *Triodopsis*	
tridentata	*t. tridentata*		*tridentata*
	t. edentilabris		
	t. juxtidens	*j. juxtidens*	*juxtidens*
		j. stenomphala	
	t. discoidea	*j. discoidea*	
	t. complanata	*c. complanata*	*complanata*
	t. tennesseensis		
platysayoides		*c. platysayoides*	
burchi			*burchi*
rugosa	*r. rugosa*		*rugosa*
	r. anteridon		
fulciden			*fulciden*
picea			*fraudulenta*
fraudulenta	*f. fraudulenta*		
	f. vulgata	*n. vulgata*	*neglecta*
neglecta		*n. neglecta*	
pendula			*pendula*
fallax	*f. fallax*	*f. fallax*	all except *claibornensis* belong to species *fallax*
	f. affinis		
palustris		*f. obsoleta*	
hopetonensis	*h. chincoteagensis*		
	h. obsoleta		
	h. claibornensis	combined with *n. vulgata*	
	h. hopetonensis		
messana		hybrid	
vannostrandi	*v. vannostrandi*		
	v. goniosoma		
	v. alabamensis	*f. alabamensis*	
vultuosa	*v. copei*	*c. copei*	*copei*
	v. henriettae	hybrid	
	v. vultuosa		
cragini		*c. cragini*	
soelneri			*soelneri*
	Subgenus: *Xolotrema*	Subgenus: *Xolotrema*	
denotata		*o. denotata*	*obstricta*
caroliniensis		hybrid	
obstricta	*o. obstricta*	*o. obstricta*	
	o. occidentalis	combined with *Mesodon sargentianus*	
fosteri	*f. fosteri*	*f. fosteri*	*fosteri*
	f. hubrichti	*f. hubrichti*	
	Subgenus: *Neohelix*	Subgenus: *Neohelix*	
albolabris	*a. albolabris*	*a. albolabris*	*albolabris*
	a. alleni	*a. alleni*	
	a. fuscolabris	intergrade	
	a. major	*a. major*	
dentifera			*dentifera*
multilineata			*multilineata*
divesta			*divesta*

TABLE XV
(*Continued*)

SPECIES	SUBSPECIES	SUBSPECIES	SPECIES
	Subgenus: *Cryptomastix*	Subgenus: *Cryptomastix*	
populi			
mullani	*m. mullani*	*m. mullani*	all except *magnidentata* belong to species *mullani*
	m. hemphilli		
	m. latilabris		
	m. tuckeri		
	m. olneyae		
	m. hendersoni		
	m. blandi		
	m. clappi	hybrid	
	m. magnidentata	combined with *sanburni*	
harfordiana		*m. harfordiana*	
sanburni			*sanburni*
devia			*devia*
germana	*g. germana*		*germana*
	g. vancouverinsulae		
TOTAL: 19 monotypic species 12 polytypic species with 41 subspecies		13 monotypic species 21 subspecies in 9 polytypic species	

ISOLATING FACTORS AND ISOLATING MECHANISMS

Geographic (spatial) isolation, as shown above, is evident in many cases in *Triodopsis*. Thus, the Appalachian Mountains caused isolation and led to speciation in *c. complanata-burchi*, *rugosa-fulciden*, and *j. juxtidens-j. discoidea*. The Mississippi Valley has been the barrier between *n. vulgata-n. neglecta*, *fallax-copei*, and *a. albolabris-a. alleni*, and the Cascade Mountains the barrier between *m. mullani-devia*. A seemingly uninhabited gap separates *c. complanata* from *c. platysayoides* (8 cases altogether). Other, less obvious, examples of geographic isolation follow. *Triodopsis j. juxtidens* and *j. stenomphala* were probably isolated by the Delaware River Valley (Fig. 9), *o. denotata* and *o. obstricta* by the Ohio River Valley (Fig. 21), and *n. vulgata* and *pendula* probably by the Appalachian Mountains (Fig. 13; the distribution of *pendula* may be secondarily altered, however; see p. 180); 3 cases altogether.

It is assumed that the following pairs were spatially isolated in the past, but the nature of the one-time barrier is not clear. The pairs are: *tridentata-c. complanata*, *f. fallax-f. obsoleta*, *f. alabamensis-f. fallax*, *f. alabamensis-f. obsoleta*, *c. copei-c. cragini*, and *m. mullani-m. harfordiana* (Figs. 3, 17, 20, 24); 6 cases altogether.

The facts that river valleys serve as barriers to dispersal, in the case of *Triodopsis neglecta*, *fallax copei*, *albolabris*, and possibly of *juxtidens* and *obstricta*, whereas the rivers themselves serve as agents of dispersal, in the case of *juxtidens* (in another part of the range) and *fraudulenta* (pp. 166, 182), at first seem contradictory. But there is no real contradiction here. The vegetation that covers the wide, often flooded valleys of the lower sections of large rivers, such as the Mississippi, Ohio, and Delaware rivers, and the fauna that lives in this vegetation, are natural barriers to species of other habitats, notably upland and mountain forests. At the same time, the smaller rivers and creeks, such as the Kanawha and the Potomac rivers and their tributaries, are just as naturally carriers downstream of the mountain-inhabiting populations.

There is insufficient information on the occurrence of behavioral and physiological isolating mechanisms. At least one of them

TABLE XVI

CLASSIFICATION ACCORDING TO DISTRIBUTION OF TWENTY CLOSELY RELATED TAXON PAIRS OF *TRIODOPSIS*.

A. MEMBERS OF PAIR SEPARATED FROM ONE ANOTHER BY A BARRIER OR GAP	BARRIER OR GAP	B. MEMBERS OF PAIR IN CONTACT, OR SLIGHTLY OVERLAPPING		C. MEMBERS OF PAIR EXTENSIVELY OVERLAPPING
c. complanata-c. platysayoides	gap of 150 miles	*j. juxtidens-j. stenomphala*	hybridize	*n. vulgata-fraudulenta*
c. complanata-burchi	Appalachians	*f. fallax* and *f. obsoleta-f. alabamensis*	"	*albolabris-dentifera*
rugosa-fulciden	Appalachians			*m. mullani-sanburni*
j. juxtidens-j. discoidea	Appalachians	*c. copei-c. cragini*	"	
n. vulgata-n. neglecta	Mississippi Valley	*o. obstricta-o. denotata*	"	
		m. mullani-m. hardfordiana	"	
fallax-copei	Mississippi Valley	*f. fallax-f. obsoleta*	intergrade	
a. albolabris-a. alleni	Mississippi Valley and gap	*a. albolabris-a. major*	"	
m. mullani-devia	Cascade Range	*tridentata-c. complanata*		
		n. vulgata-pendula		
TOTAL: 8		9		3

must be responsible for the separation of *tridentata* from *c. complanata*, *j. juxtidens*, and *f. fallax*. Ecological isolating mechanisms are not involved (p. 153). Ecological isolation is, in any case, rare in *Triodopsis*. The only examples I know of are between *tridentata* and *c. platysayoides*, *tridentata* and *j. discoidea*, and the Virginia populations of *j. juxtidens* and *j. stenomphala*. Apparently ecological divergence develops much more slowly than morphological divergence in *Triodopsis*. The numerous cases of ecological exclusion which result when two sympatric species have similar or identical ecological preferences are witness to this statement. Ecological exclusion was found between *tridentata* and *c. complanata*, *tridentata-j. juxtidens*, *tridentata-j. discoidea*, *tridentata-f. fallax*, *j. juxtidens-f. fallax*, *j. juxtidens-f. obsoleta*, *o. denotata-fosteri*, and perhaps *a. alleni-multilineata* (8 or perhaps 9 cases altogether). As a rule, behavioral or physiological isolating mechanisms also develop more slowly than do morphological differences, as shown by the long list of the secondarily interbreeding populations (see below); in some cases, however, they may develop concomitantly with morphological differences, *e.g.*, between *tridentata* and *c. complanata*, *n. vulgata* and *fraudulenta*, *n. vulgata* and *pendula*, *dentifera* and *a. albolabris*, *sanburni* and *m. mullani*.

HYBRIDIZATION

The term hybridization is defined by Mayr (1963: 110) as "the crossing of individuals belonging to two unlike natural populations that have secondarily come into contact." He distinguishes various kinds of hybridization. In *Triodopsis*, the kind he describes as allopatric hybridization is common. It is found in 5, or possibly 7, of the 22 species: in *juxtidens*, *fallax* (between *f. alabamensis* and both *f. fallax* and *f. obsoleta*), *copei*, *obstricta*, and *mullani*, and possibly in *neglecta*, *fallax* (between *f. fallax* and *f. obsoleta*), and *albolabris*.

Hybrids are conventionally recognized by comparing the coefficients of variation; populations with high coefficients of variation are considered hybrids, those with normal coefficients, parents. This method could not be employed in *Triodopsis*, since one of the putative parents always had higher coefficients than both the putative hybrids and the other parent (Fig. 26). To overcome this difficulty, the range of variation of the various populations was compared. The comparison was made by two slightly different methods. Either the

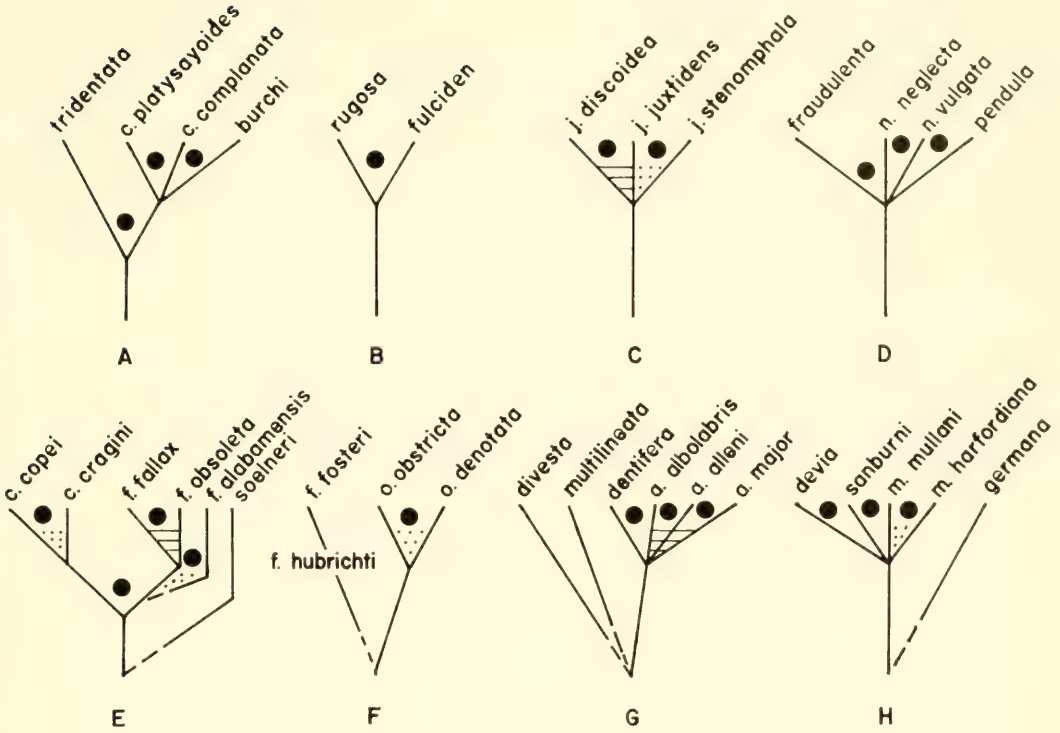

Figure 25. Assumed evolutionary relationships in *Triodopsis*. Solid dots mark the 20 closely related taxon pairs, utilized in making up Table XVI. Stippling indicates hybridization; horizontal lines, primary intergradation; dashed line, uncertain relationship.

range was plotted against population size (Fig. 27), or the natural samples were converted into samples of standard size, and the range of variation of these standardized samples was calculated and compared (Fig. 4; method adapted from Simpson, 1941). The advantage of the first method was that it avoided the use of the standard deviation, which is high in samples with a skewed distribution curve, and which, as may be recalled, is the situation in many hybrid populations of *Triodopsis*. The advantage of the second method is its clarity. Both methods were used for species in which samples with skewed distribution curves occurred. The second method was used alone in species with normal distribution curves.

The samples which showed considerably greater variability than the average were considered hybrids. These samples were always intermediate between two "parental" taxa, and they always occurred in the zone of contact between the two, or in a ring along the periphery of one of them (the latter also can be considered a contact zone, if we assume that one taxon is presently in the process of surrounding the other one). The morphological intermediacy and the described distribution pattern are consistent with the interpretation that the populations in question are of hybrid origin.

The range of variation in the hybrid populations is wider than normal, but it never spans the entire range of variation of the species, as is the case in some other hybrids. This may be because most of the characters utilized in the analysis of variation are polygenic; such characters often do

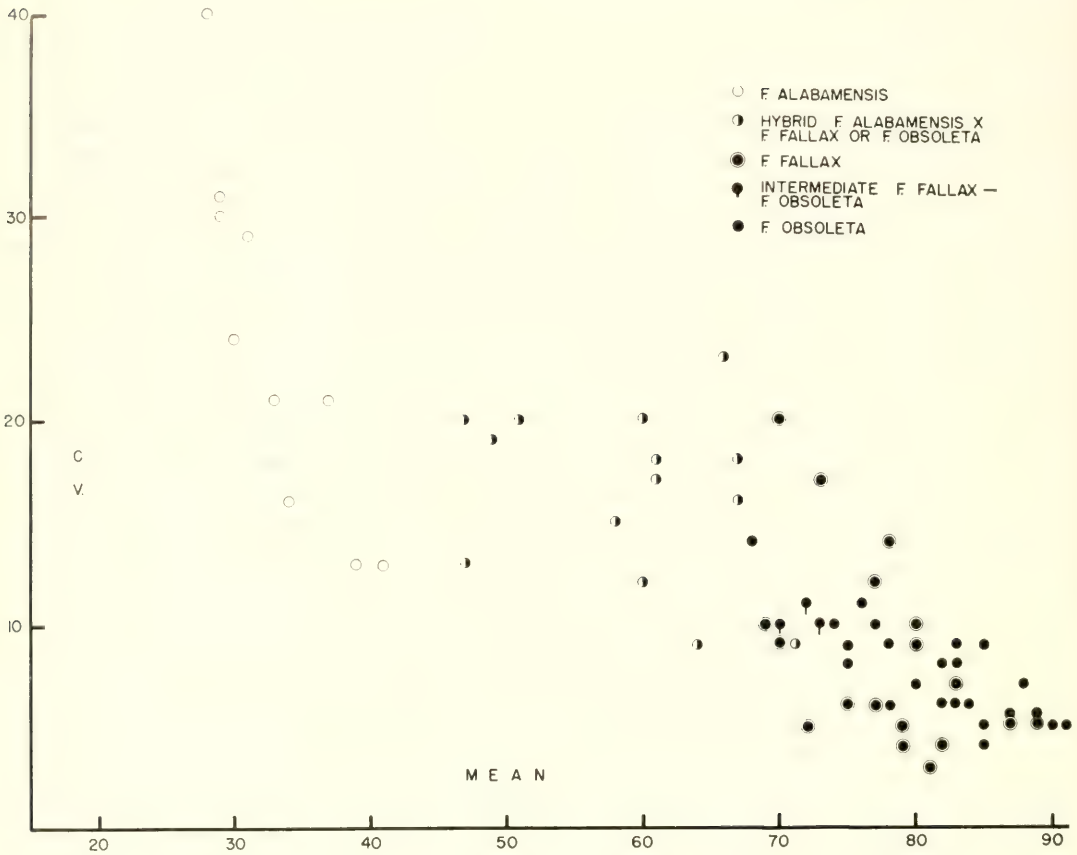

Figure 26. Scatter diagram of coefficient of variation (C.V.) versus mean in samples of *Triodopsis fallax*. Scale in character index units. The coefficient of variation tends to be inversely proportional to the mean. This is contrary to the expectation that hybrid samples will show higher coefficients than do the parental samples.

not show an appreciable increase in variation (Mayr, 1963: 131, 377).

It is possible that even supposedly "pure" populations of *T. f. alabamensis* have incorporated some genes from *f. fallax* or *f. obsoleta*. The populations of *f. alabamensis* are definitely more variable than those of *f. fallax* or *f. obsoleta* (Figs. 4, 27); a specimen of *f. alabamensis* from the interior of the range has a fulcrum, which normally occurs only in *f. fallax*. As the range of *f. alabamensis* is rather limited, it is easy to imagine that occasional specimens of *f. fallax* or *f. obsoleta* reach the heart of its range and interbreed there with the local *f. alabamensis* populations. This phenomenon approaches what is referred to as introgression by Anderson and Hubricht (1938). To use the term, however, would not be quite justified, because in our case only subspecies are involved, whereas introgression is usually applied to cases involving distinct species.

Adaptiveness of geographic variation

Those characters that appear in several, not directly related species, occupying the same area or habitat, can be considered adaptive to the particular area or habitat (Moore, 1949). In addition to such fundamental features as having a shell, coiling, etc., there are two shell characters in *Trio-*

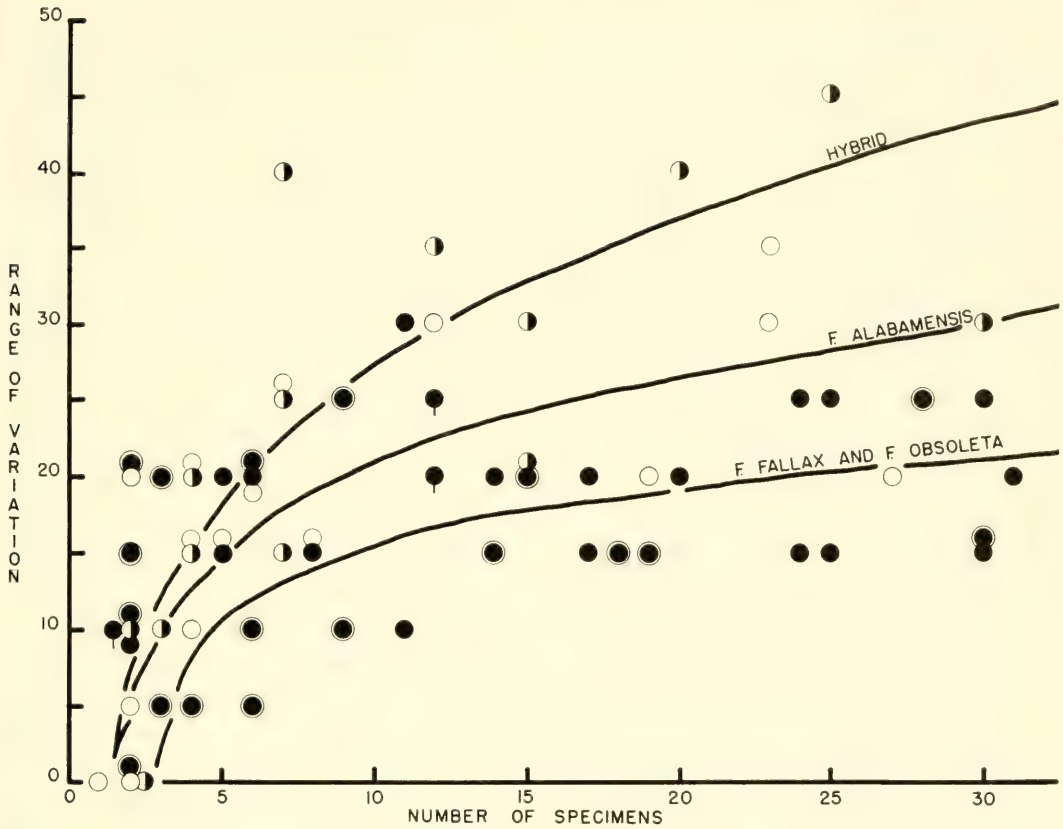

Figure 27. Scatter diagram of the range of variation in character index versus number of specimens in samples of *Triodopsis fallax*. Vertical scale in character index units. The hybrid samples have the widest range of variation, *f. alabamensis*, narrower, *f. obsoleta* and *f. fallax*, narrowest. Curves fitted by eye.

dopsis which satisfy the above requirements. One is the strong armature in mountainous areas, the other, the smooth sculpture in valleys.

Heavy armatures are observed in six species in *Triodopsis*. These are: *T. tridentata*, grades C and D, *rugosa, fraudulenta, f. fallax, c. copei* and *m. mullani*. Five of these forms occur in mountainous habitats; thus, *tridentata, rugosa* and *fraudulenta* in the Appalachians, *f. fallax* in the Blue Ridge Mountains, and *m. mullani* in the Cascade Range and the Rockies. The sixth form, *c. copei*, occurs however at low elevations, below 500 feet, in Texas (Fig. 20). The reason for its peculiar distribution is not known. Another anomaly is that *T. f. fallax* does not reach the peak region, but stops at about 1500 feet of elevation (Figs. 14, 15).

In spite of these two exceptions, it seems safe to conclude that the heavy armature is an adaptation to the mountainous habitat. This conclusion is supported by the case of *T. tridentata*, grades C and D, and *fraudulenta* and *f. fallax*. These three forms occur strictly allopatrically in the Appalachian and Blue Ridge Mountains (Fig. 14). They do so probably because they are all mountain-adapted, and thus they would compete for habitats with each other if they occurred sympatrically.

There is no explanation, however, of the significance of the heavy armature in moun-

tainous conditions. The explanations proposed so far appear unlikely. For instance, Clench (personal communication) suggested that the large lip teeth and parietal lamella may be a protection against predators such as the beetles of the genus *Cychrus* and *Calosoma* (Ingram, 1950), because they obstruct the aperture and thereby make the entry of the predator difficult or impossible. However, there is no clear correlation between the occurrence of the predatory beetles and the heavy armature in the snails; the former occur in lowlands and mountains as well, the latter, only in the mountains (except *c. copei*). Thus Clench's suggestion cannot be the entire explanation, although it is not impossible that the heavy armature does give some protection against predators. Another obvious explanation could be that the strong armature depends upon the abundance of lime in the soil. But this idea also can be dismissed; heavy armature occurs on all kinds of rocks. Archer (1938), who also noticed the correlation between the armature and the elevation, did not produce any good explanation of the phenomenon. Knipper's conclusion (1939) that the armature is light in moist conditions and heavy in dry, apparently does not apply to *Triodopsis*, because the higher we go in the mountains the greater the precipitation. And even if it applied to *Triodopsis*, it could not be the explanation we are looking for, because it is simply another statement of an observation, not an explanation. It should be mentioned that Knipper studied European helicine and helicigonine snails, whereas Archer and I studied North American polygyrids (*Stenotrema* and *Triodopsis*, respectively); this may explain why Knipper found a correlation between armature and dryness, Archer and I, a correlation between armature and elevation.

The other apparently adaptive character is the smooth sculpture of the shell. It occurs in four or possibly five species in *Triodopsis*, that live in valleys, on the river banks, or near the river. Thus *T. c. complanata* has smooth populations in the valley of the Cumberland River, in Kentucky; *burchi* lives in the Dan River valley, in Virginia; *j. discoidea*, in the Ohio and Mississippi valleys, in Ohio and Missouri; and *c. platysayoides*, in the canyon of the Cheat River, in West Virginia. *Triodopsis m. mullani* also has smooth shelled populations, but the exact habitat of these populations is not known. These observations are comparable with Rensch's findings (1932). He wrote that land snails tend to have smooth, glossy, brown shells in cold climates, and white or strongly sculptured shells in hot ones. Why a smooth sculpture should be advantageous in cold climates or on the river banks remains, however, unknown.

Irregularity of geographic variation

According to Mayr (1963: 361), much of the geographic variation is clinal in continental species. Two of his main reasons are that (1) the selective factors (e.g., climate) change gradually, and thus the characters they act upon also tend to change gradually, and (2) gene flow tends to smooth out differences between adjacent populations.

In *Triodopsis*, however, very few clines occur. Eleven taxa are distributed over very restricted areas, and thus could not possibly develop clines. In the remaining 23 taxa, a total of 86 characters were measured and mapped; the characters included aperture, sculpture, keel, fulcrum, shell width, height to width ratio, umbilicus to width ratio, whorl to width ratio, and upper lip tooth to lower lip tooth ratio. Only eight characters (9.3%) vary clinally. Five clines are clear cut: the upper lip tooth to lower lip tooth ratio, in *tridentata*; the umbilicus to width ratio, in *rugosa*; size (width), in *j. discoidea*; aperture, from *f. obsoleta* to *f. fallax*; and whorl to width ratio, in *germana*. Three clines are less clear cut: the size and aperture, in *tridentata*, and the height to width ratio, in *a. alleni*. It is possible that the umbilicus to

width ratio of *rugosa* should also be listed with the second group. As examples of clines, the variations of the umbilicus to width ratio in *T. rugosa*, and of the size (shell width) in *T. j. discoidea* are illustrated (Figs. 7, 12). Irregular geographic variation is exemplified by the variation of size and sculpture in the former and that of sculpture in the latter taxon (Figs. 8, 12).

The scarcity of clines in *Triodopsis* is evidently at variance with the expectation. The probable explanation is as follows. First, selective forces different from those affecting large animals act upon *Triodopsis* (or, speaking generally, upon small animals). Thus, for small animals the microclimatic factors are of prime importance, whereas for large ones, the macroclimatic factors are the most important. Second, the forces acting upon small animals vary more irregularly than those acting upon large ones. It is easy to see that the microclimate of a cool and humid northern slope contrasts sharply with that of a warm and dry southern slope, or that of an open plateau with that of a ravine; all of these places may, of course, share a very similar macroclimate. Since such habitats may occur repeatedly within one area, the resulting irregular variation is only to be expected.

It is most unlikely that absence of gene flow would cause the irregularity of geographic variation in *Triodopsis,* even though land snails are often (I think unjustifiably) cited as examples of sedentary species. Gene flow is observable in several species. Cases in which the hybrids form a ring around the range of subspecies A (Figs. 17, 20, 21) can best be explained by immigration (gene flow) from subspecies B into the scarcely inhabited, peripheral area of subspecies A, and subsequent interbreeding there between B and A. The gene flow cannot, of course, be restricted only to the peripheral areas, but must also occur inside the range. Additional evidence of the occurrence of gene flow is the fact that the hybrid zone between *j. juxtidens* and *j. stenomphala* does not quite coincide with the valley of the Delaware River, which presumably was once the isolating barrier between them, but lies east of that valley (Fig. 9). It seems that there is a "gene overflow" from the side of *j. juxtidens* toward *j. stenomphala* (the latter has a much smaller population), across the Delaware River valley. The "introgression" from *T. f. fallax* to *f. alabamensis* also supplies evidence of gene flow, as discussed above. Thus irregular geographic variation apparently occurs in spite of gene flow, not because of a lack of it.

SUMMARY

(1) With the use of quantitative methods and the application of the biological species concept, the systematics of the genus *Triodopsis* has been revised. One species has been divided into three separate species, and a new subspecies has been described. Nevertheless, because of repeated synonymizations the number of taxa has been reduced from 60 to 34, that of the species from 31 to 22. In detail, the number of monotypic species has been reduced from 19 to 13, polytypic species from 12 to 9, and subspecies from 41 to 21.

(2) There is overwhelming evidence that speciation in *Triodopsis* is predominantly geographic. Of 20 analyzed cases, this is virtually certain in 8, very likely in 9, probable in 2, undecided in 1. Geographic isolating barriers are common. Thus, the Appalachian Mountains served as such in 4 of the 20 analyzed cases, the Cascade Mountains in 1, the valley of the Mississippi River in 3, the Ohio River in 1, the Delaware River in 1, a gap between the two speciating populations in 1; in only 6 cases can no obvious geographic barrier be discerned (3 cases overlap).

Reproductive or behavioral isolation, but particularly ecological isolation, may develop much more slowly than do morphological differences, and one kind of isolating mechanism may precede the other. For this reason, the "yardstick method" of judg-

ing the degree of biological distinctness solely on the basis of morphological distinctness has been abandoned.

(3) Allopatric hybridization is common in *Triodopsis*. It occurs in 5 or possibly 7 of the 22 species. Some authors have considered as taxonomically distinct some of the hybridizing populations or the hybrids. However, these taxa have not reached either reproductive or ecological isolation; this opinion, therefore, is apparently incorrect.

The hybrid populations are recognized by their greater variation, morphological intermediacy, and occurrence in the zone of contact between the parental populations. The range of variation was used for ascertaining the extent of variation; coefficients of variation could not be used for such purposes.

(4) A strong development of the aperture appears to be an adaptation to mountainous habitats, a smooth shell sculpture an adaptation to valley habitats. Strong armature is found in 6 of the 22 species, smooth sculpture in 4. The significance of these adaptations is unknown.

(5) The geographic variation is predominantly irregular. Only 8 clines have been found among the 86 cases analyzed. This is unexpectedly few in continental species. It is theorized that the irregularity of the geographic variation is due to irregularly changing factors such as the microclimate. The notion that lack of gene flow is responsible is rejected; gene flow is evidenced by the ring-shaped distribution of hybrids around some subspecies, "gene overflow" from *T. j. juxtidens* to *j. stenomphala* across the Delaware River valley, and "introgression" from *T. f. fallax* and *f. obsoleta* into *f. alabamensis*.

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(Received 25 August 1964)

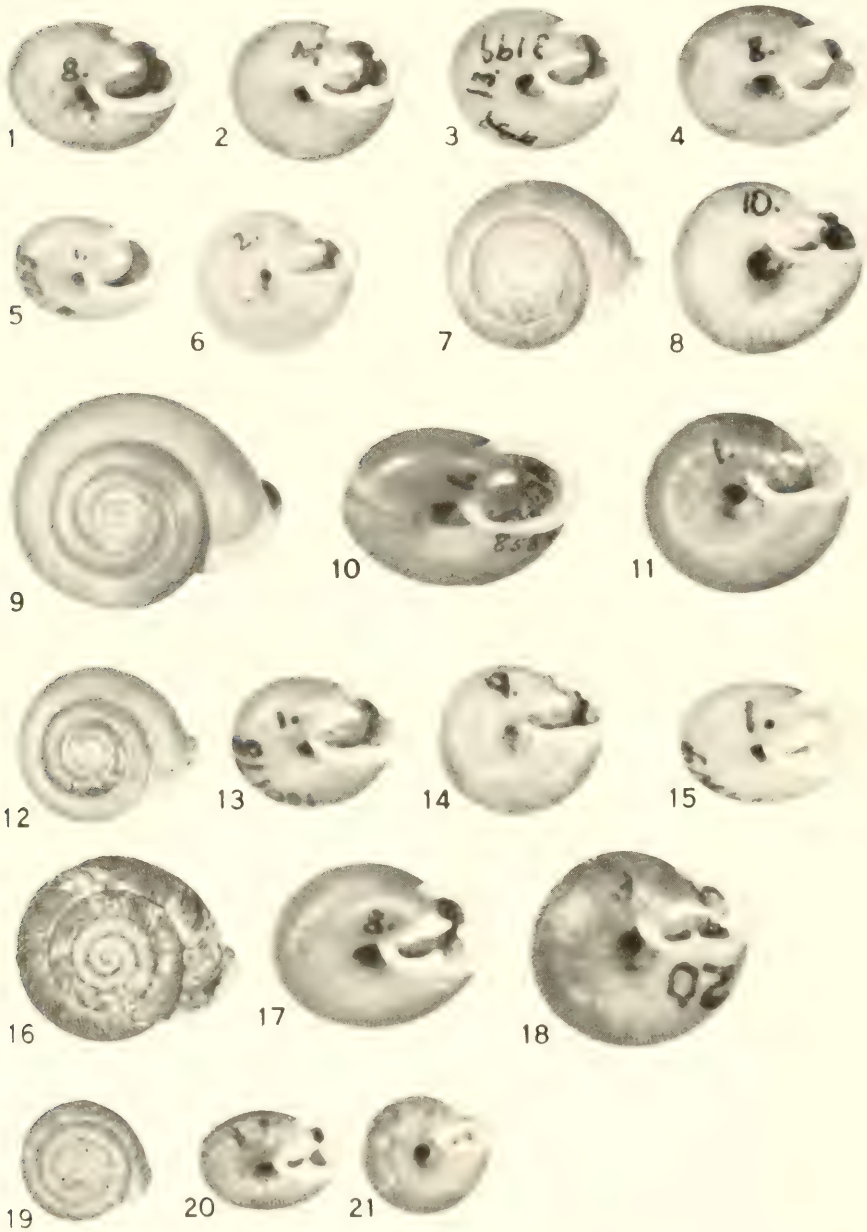

Plate I. The *Triodopsis tridentata* and *rugosa* complexes. 1–8, *Triodopsis tridentata*: 1 and 7, aperture grade A, Williston, Vermont; 2, aperture grade B, Bethel, Pennsylvania; 3, aperture grade C, Moores Hill, Indiana; 4 and 8, aperture grade D, Murphy, North Carolina; 5–6, *edentilabris*, considered synonymous with *tridentata*, aperture grade A, types, "Cumberland Mountains." 9–11, *Triodopsis c. complanata*: 9–10, Jamestown, Kentucky; 11, Boone, Tennessee. 12–14, *Triodopsis burchi*: 12 and 14, paratypes; 13, holotype, Danville, Virginia. 15–18, *Triodopsis rugosa*: 15, paratype, Blair, West Virginia; 16, Big Stone Gap, Virginia; 17–18, *anteridon*, considered synonymous with *rugosa*, paratypes, Valley Forge, Tennessee. 19–21, *Triodopsis fulciden*, Conover, North Carolina. Figures 1–8 are magnified × 1.6; figures 9–11, × 1.5; figures 12–21, × 2.2.

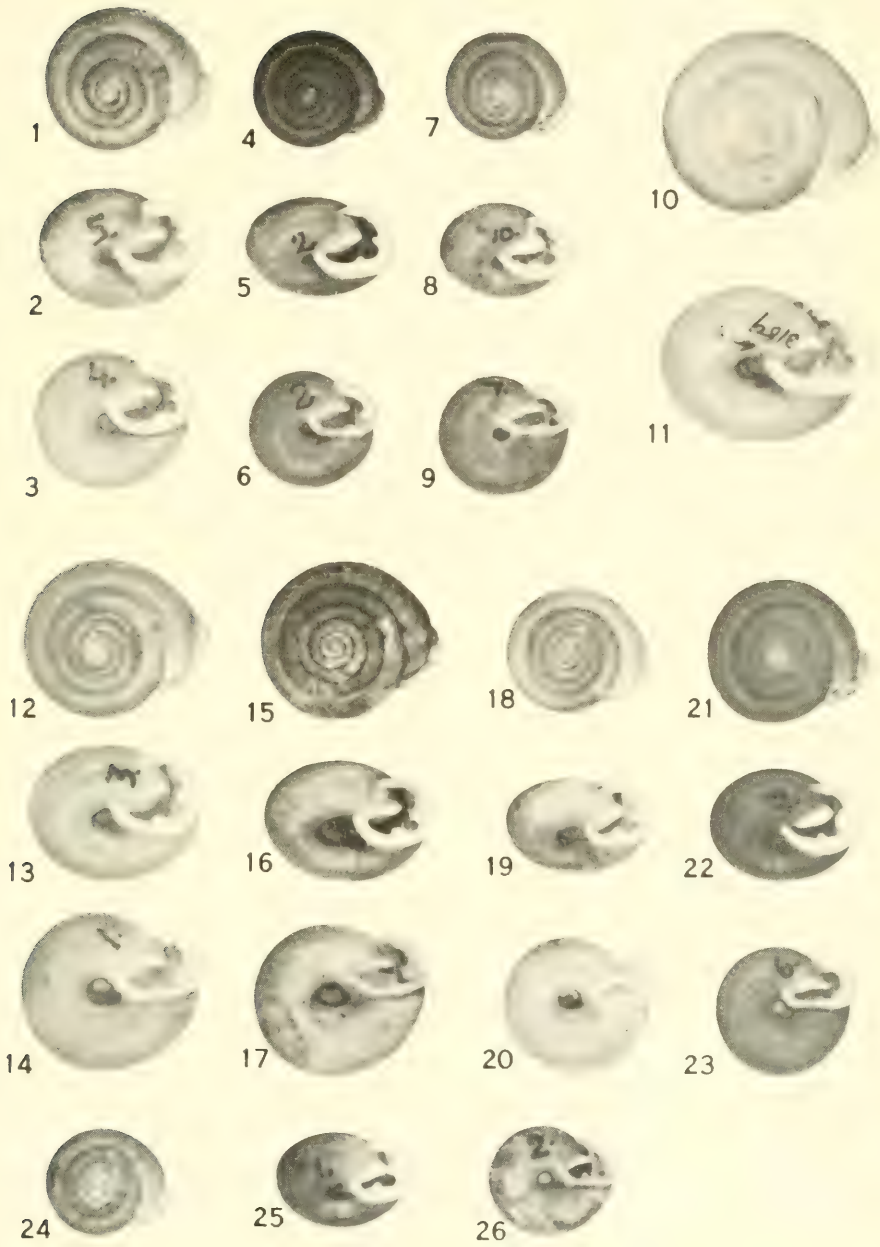

Plate II. The *Triodopsis juxtidens* and *fraudulenta* complexes. 1–11, *Triodopsis juxtidens*: 1–2, *j. juxtidens*, Flatbrookville, New Jersey; 3, *j. juxtidens*, Richmond, Virginia; 4 and 6, hybrid *j. juxtidens* × *j. stenomphala*, Bedford, Virginia; 5, hybrid, Newark, New Jersey; 7, *j. stenomphala*, Dry Fork, Virginia; 8–9, Jenkintown, Pennsylvania; 10–11, *j. discoidea*, Cincinnati, Ohio. 12–20, *Triodopsis neglecta*: 12–14, *n. vulgata*, Ann Arbor, Michigan; 15–17, *n. vulgata* approaching *n. neglecta*, Huntsville, Alabama; 18–20, *n. neglecta*, Eureka Springs, Arkansas. 21–23, *Triodopsis fraudulenta*, Lewisburg, West Virginia. 24–26, *Triodopsis pendula*: 25, holotype; 24 and 26, paratypes, Hanging Rock State Park, North Carolina. Figures 1–9 and 12–26 magnified × 1.5; 10–11, × 1.9.

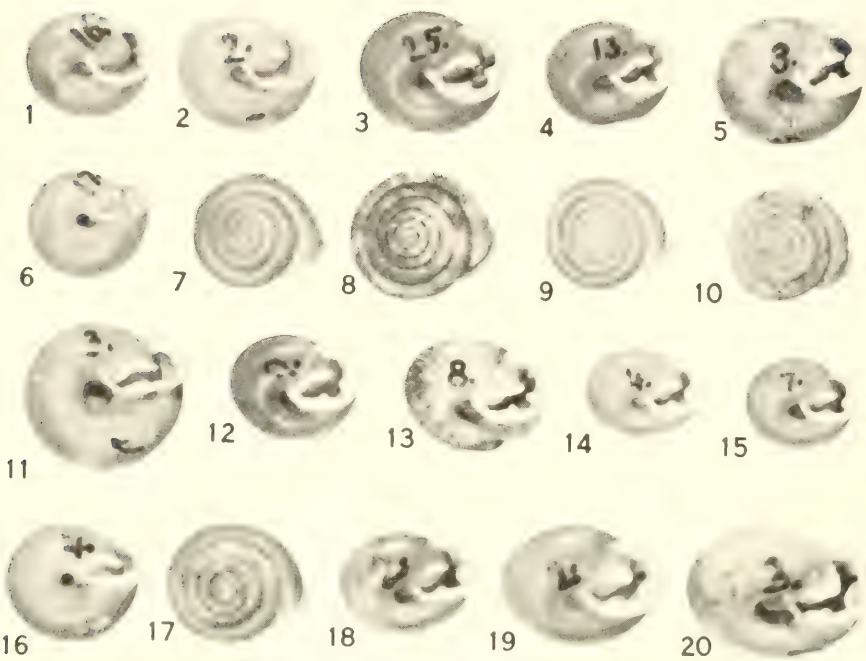

Plate III. The *Triodopsis fallax* complex. 1–15, *Triodopsis fallax*: 1, 6, and 7, *f. obsoleta*, aperture grade A, Trenton, North Carolina; 2, *f. obsoleta*, paratype, aperture grade A, Newbern, North Carolina; 3, *f. obsoleta*, aperture grade B, Rich Square, North Carolina; 4, *f. fallax*, aperture grade C, Marion, South Carolina; 5, *f. fallax*, aperture grade D, Seagrove, North Carolina; 10, *f. fallax*, aperture grade D, Chestertown, Maryland; 11, *f. fallax*, aperture grade D, Draper, North Carolina; 8 and 13, hybrid of *f. alabamensis* with *f. fallax* or *f. obsoleta*, or intermediate between the latter two subspecies, Aiken, South Carolina; 12, hybrid, Hartwell, Georgia; 9, 14, and 15, *f. alabamensis*, Langdale, Alabama. 16–20, *Triodopsis copei*: 16, *c. cragini*, aperture grade B, Arkadelphia, Arkansas; 17–18, *c. cragini*, aperture grade B, Chetopa Creek, Kansas; 19, hybrid *c. cragini* × *c. copei*, aperture grade C, Macdona, Texas; 20, *c. copei*, aperture grade D, Neches, Texas. Figures 1–15 are magnified × 1.5, 16–20 × 2.

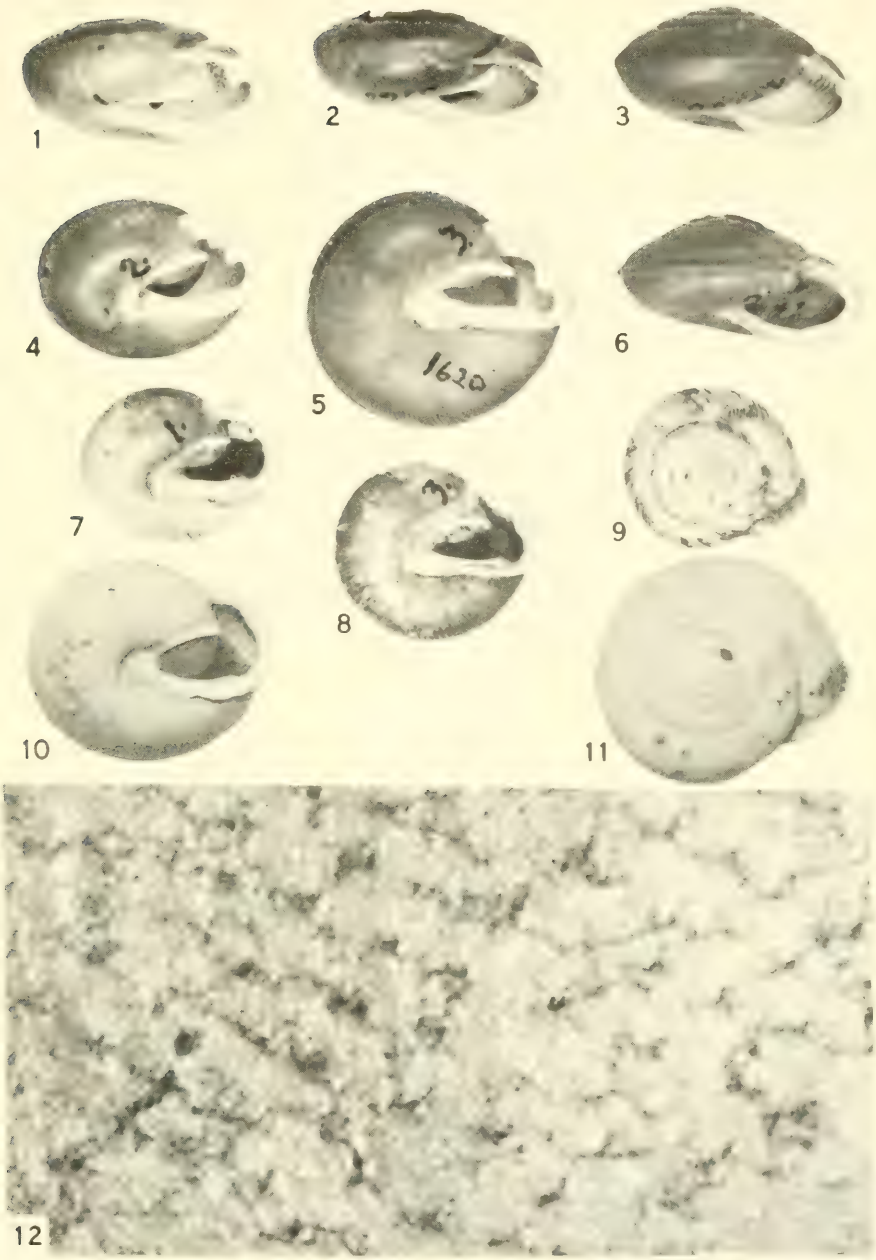

Plate IV. The *Triodopsis obstricta* complex. 1–6 and 12, *Triodopsis obstricta*: 1 and 4, o. *denotata*, angularity # 1, North Adams, Massachusetts; 2, hybrid o. *obstricta* × o. *denotata*, angularity # 2, Mt. Carmel, Illinois; 3, hybrid, angularity # 3, Frierson Mills, Louisiana; 5–6, o. *obstricta*, angularity # 4, Nashville, Tennessee; 12, sculpture of o. *denotata*, a portion of the last whorl shown, Annandale, New York. 7–11, *Triodopsis fosteri*: 7–9, *f. fosteri*, paratypes, Elizabethtown, Illinois; 10–11, *f. hubrichti*, paratypes, Valmeyer, Illinois. Figures 1–6 are magnified × 1.5; 7–9, × 1.6; 10–11, × 1.4; 12, × 40.

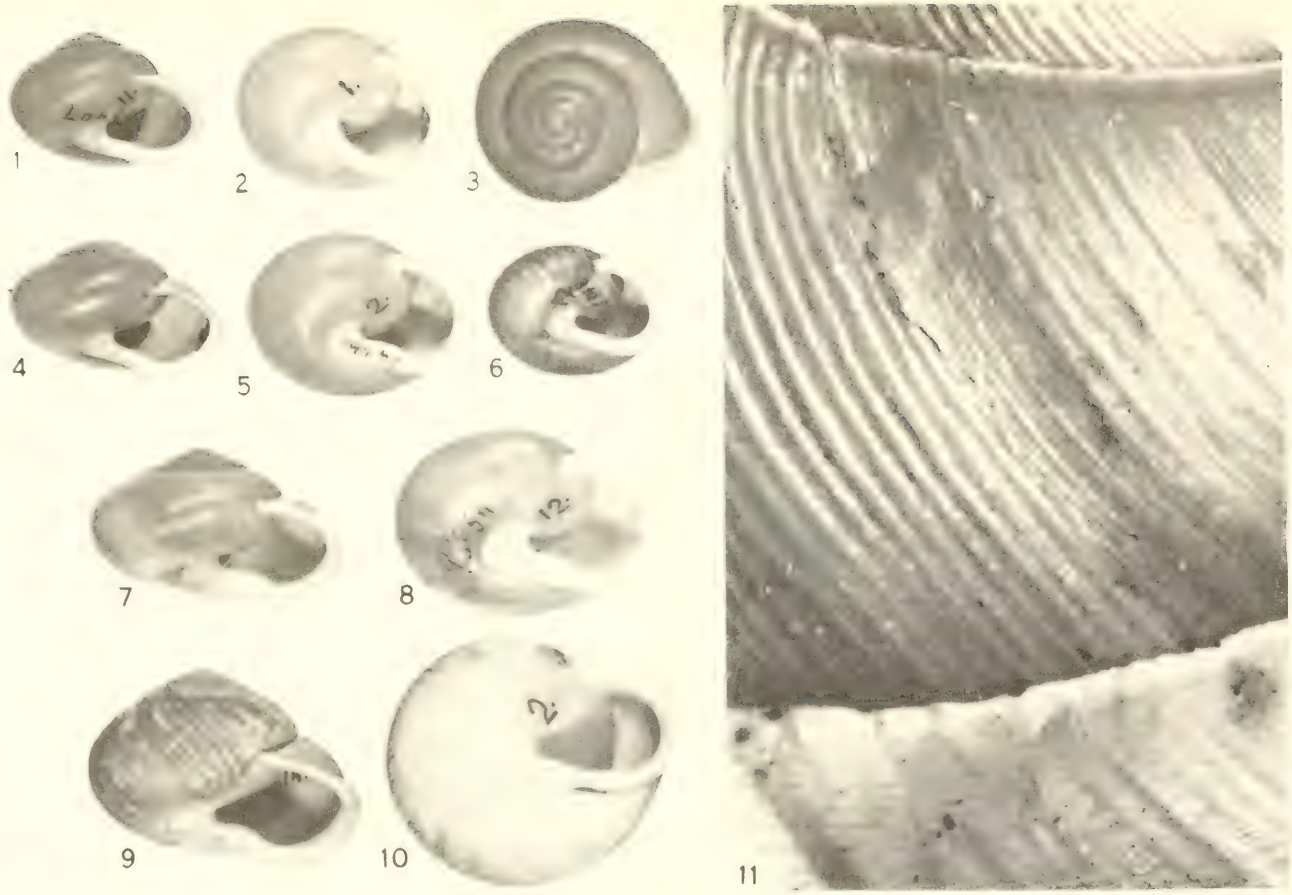

Plate V. *Triodopsis albolabris*. 1 and 3, *T. a. albolabris*, Orono, Maine; 2, *dentata*, Circleville, Ohio; 6, *maritima*, Biological Station, Michigan; the latter two forms are considered synonymous with *a. albolabris*; 11, sculpture of *a. albolabris*, portions of the last three whorls shown, with a breakage in the penultimate whorl (notice how much coarser the spiral lines become after the breakage); 4, *a. alleni*, Hamilton, Illinois; 5, *a. alleni*, paratype, Eureka Springs, Arkansas; 7, *fuscolabris*, considered intermediate between *a. alleni* and *a. major*, Woodville, Alabama; 8, *fuscolabris*, Huntsville, Alabama; 9, *a. major*, Murphy, North Carolina; 10, *a. major*, Elamville, Alabama. Figure 11 magnified × 15; all other figures, × 1.

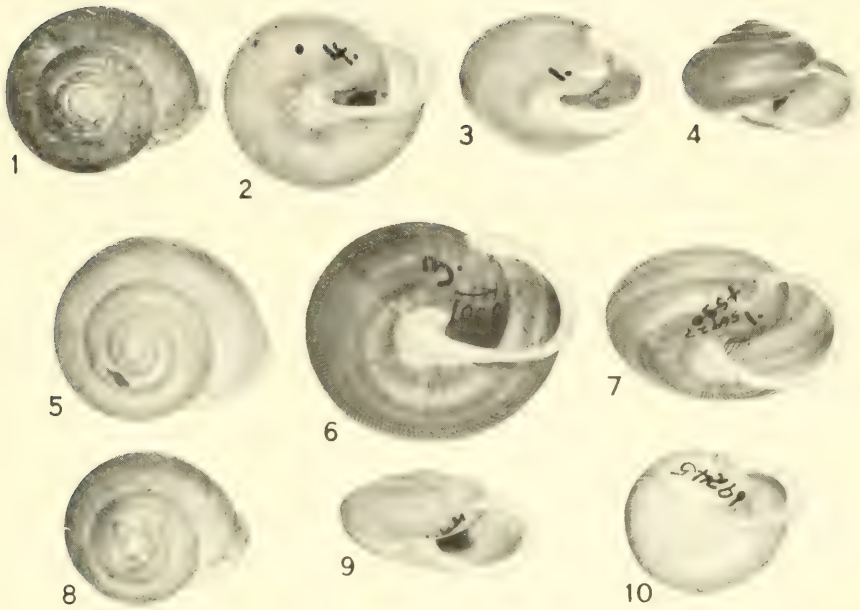

Plate VI. *Triodopsis dentifera, multilineata,* and *divesta.* 1–3, *Triodopsis dentifera:* 1, Rangeley, Maine; 2, Carrigain [or Cardigan?] Mountain, New Hampshire; 3, Vermont, labelled as "? cotype." 4–7, *Triodopsis multilineata:* 4, *algonquinensis,* cotype, considered synonymous with *multilineata,* Algonquin, Illinois; 5, Cincinnati, Ohio; 6, Mt. Carmel, Illinois; 7, Bluffton, Indiana. 8–10, *Triodopsis divesta:* 8, Hot Springs, Arkansas; 9, "Oklahoma"; 10, Cherokee County, Oklahoma. All figures magnified × 1.35.

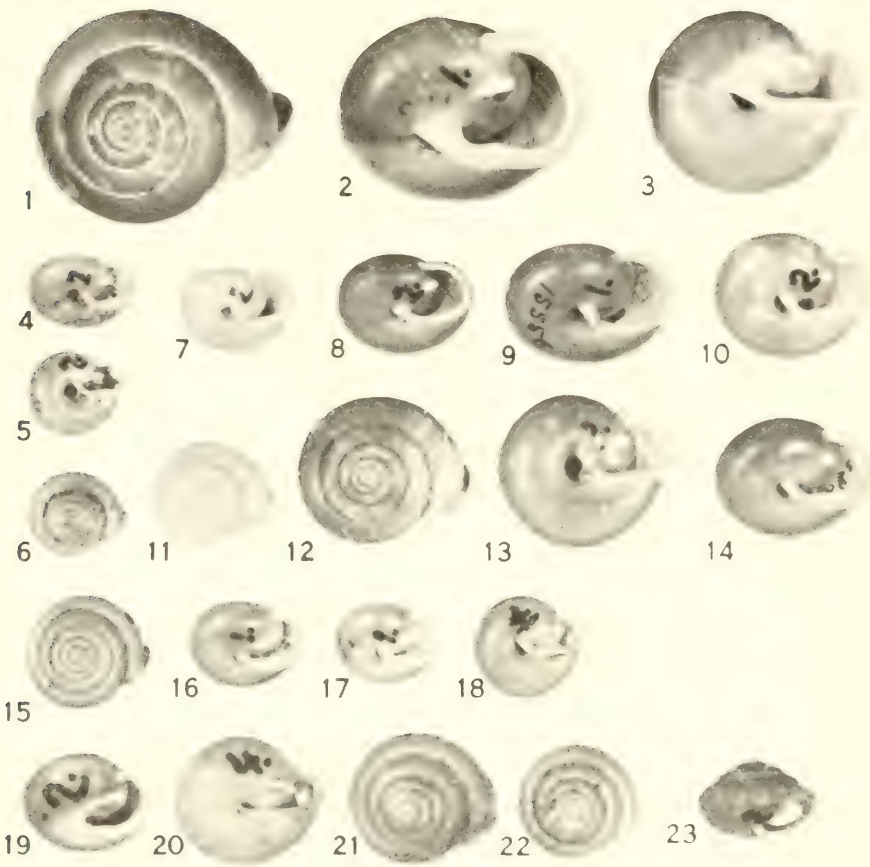

Plate VII. The *Triodopsis mullani* complex. 1–3, *Triodopsis devia*, Olympia, Washington. 4–14, *Triodopsis mullani*: 4–6, *m. harfordiana*, Salmon River, Idaho, 4 and 6 cotypes; 7 and 11, hybrid *m. harfordiana* × *m. mullani*, Salmon River, Idaho; 8, *blandi*, Post Falls, Idaho; 9, *hendersoni*, Weiser, Idaho; 10 and 13, *olneyae*, Selway Falls, Idaho; 12, *olneyae*, Libby, Montana; 14, *olneyae*, "Idaho"; the latter three forms are considered synonymous with *m. mullani*. 15–18, *Triodopsis sanburni*: 15 and 18, Kingston, Idaho; 16, Coeur d'Alene Mountains, Idaho; 17, Old Mission, Idaho. 19–23, *Triodopsis germana*: 19, Knapton, Washington; 20–21, Astoria, Oregon; 22–23, *vancouverinsulae*, considered synonymous with *germana*, Vancouver, British Columbia. Figures 1–18 magnified × 1.45; 19–23, × 2.30.

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Bulletin OF THE
Museum of
Comparative
Zoology

Pipid Frogs from the Early Cretaceous of Israel and Pipid Evolution

EVIATAR NEVO

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 8
FEBRUARY 12, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

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PIPID FROGS FROM THE EARLY CRETACEOUS OF ISRAEL AND PIPID EVOLUTION

EVIATAR NEVO[1]

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ABSTRACT

The discovery of a horizon rich in frogs in the lower early Cretaceous of Makhtesh Ramon, Israel, is recorded, and the geology, age, paleoecology, fauna, flora, and climate are discussed. Articulated frog skeletons comprise most of the fauna. They are described as two new pipid genera including three species: *Thoraciliacus rostriceps*, 800 specimens; *Cordicephalus gracilis*, 49 specimens; and *Cordicephalus longicostatus*, 14 specimens. All species are aquatic, variable, and represent a melange of 21 primitive and 16 specialized characters. In all, the pelvis, skull, and pectoral girdle are highly variable, the limbs less so. The skull, pelvis, and limbs are essentially specialized, the column and pectoral girdle primitive. *Thoraciliacus* is more aquatic, variable, and specialized than *Cordicephalus*, yet both are the most primitive and earliest sure pipids known. The thoraciliacid line is related to South American and African Cretaceous pipoids; it flourished in the Cretaceous, and became extinct in the Tertiary, while *Cordicephalus* is on the ancestral line of Tertiary xenopids. Reevaluation of pipid classification does not support a separate family for Cretaceous pipoids which may be referred to Recent Pipidae.

Ramon pipids suggest that pipids pursue a progressive primary aquatic adaptation, this operating as the main evolutionary selective factor since their probable Triassic origin from proanurans. Pipids have probably never been taxonomically prolific, but their record suggests a rapid basic diversification, extinctions, and slower later evolution. Evo'utionary trends since early Cretaceous times involve a series of structural changes, explicable as progressive improvements in aquatic adaptations. Pipids had an almost worldwide distribution in Cretaceous and probably Upper Jurassic times, but their center of origin is still obscure.

INTRODUCTION

The fossil record of Anura is traceable back to the early Jurassic, yet our ideas of the evolution of frogs are still mainly de-

[1] Department of Zoology, The Hebrew University, Jerusalem, Israel.

rived from studies of Recent forms (Griffiths, 1963; Tihen, 1965). This fact stems from a general conviction that the fossil record is incomplete, that fossil frogs are scarce, and that those known are essentially modern in their osteology. The first of these views is still justified so far as the early, presumably Triassic, transition period from proanurans to anurans is concerned. The gap between the earliest known true frog, *Vieraella herbstii* (Reig, 1961) from the Lower Jurassic of Argentina, and the possible ancestor, *Triadobatrachus massinoti* (Piveteau, 1937) from the Lower Triassic of Madagascar, is still neither documented by fossils nor in any way illuminated by Recent frogs. This gap can only be expected to be bridged, at least in part, when future finds from continental Triassic deposits unveil the transitional forms which linked proanurans to anurans.

However, recently discovered fossil evidence (Nevo, 1956, 1964b; Reig, 1957, 1959, 1961; Hecht, 1963; Casamiquela, 1961a, b, 1965; Špinar, 1963; Estes, 1964) has partly elucidated patterns of Jurassic and Cretaceous frog evolution. Our knowledge of early anuran history has greatly increased during the last few years and has been partly reviewed by Hecht (1963). Significantly, the recent finds of large collections, involving complete frog skeletons, consist mainly of aquatic forms from the Cretaceous of South America, South Africa, Asia, and the Tertiary of Europe. Most other fossil frogs are fragmentary, apparently the result of the preservation characteristic of terrestrial habitats.

The available record of fossil frogs confirms in part earlier evolutionary hypotheses based on Recent forms, negates others, and contributes to the postulation of new ideas. It suggests the Triassic as the transition period from proanurans to anurans. It indicates the existence of three (and implies the presence of a fourth) independent anuran offshoots in Jurassic times consisting of the families Ascaphidae, Discoglossidae, Pipidae, and possibly some more advanced frog families. The record suggests two major adaptive radiations: first, an aquatic radiation during the Triassic and Jurassic; second, a terrestrial one during Jurassic and Cretaceous times continuing into the Tertiary. Finally, the record suggests possibilities for the objective evaluation of variation, evolutionary trends, phylogenetic and paleogeographic patterns.

The present paper is a first part of population studies on a collection of early Cretaceous frogs from Makhtesh Ramon, Israel (Nevo, 1964b). The amphibian zone, encountered accidentally during geological studies in Makhtesh Ramon in 1954 (Nevo, 1956), has already yielded 863 post-metamorphic, mostly articulated, frogs, one tadpole, and recently 14 urodeles (Nevo, 1964a). The frog collection consists of two genera comprising three species of aquatic pipid frogs. This paper describes the geology, environment and age of the amphibian bed, and the morphology and systematic relationships of the new forms. Pipoid classification is reviewed, suggesting that all hitherto known Cretaceous pipoids should be allocated to the Recent family Pipidae. Finally, the phylogeny, evolutionary trends and paleogeography of pipoids as suggested by this study are presented.

It is my conviction, explicitly reflected in the population studies, that the available fossil record of frogs, particularly of aquatic forms, is more complete than has been realized and that it permits a more objective approach to evolutionary studies. Furthermore, as I will later report, the Ramon collection proved suitable for demographic analysis both intra- and interspecifically, providing insight into population structure and dynamics of Cretaceous pipid frogs.

ACKNOWLEDGMENTS

This paper is part of a thesis submitted to the Department of Zoology of The Hebrew University of Jerusalem as partial fulfillment of the requirements for degree of Doctor of Philosophy, March 1964. The

manuscript was revised and completed during tenure of a Committee on Evolutionary Biology Traineeship at the Museum of Comparative Zoology.

This study was carried out under the guidance of Professor G. Haas, to whom I am especially grateful for his encouragement and great interest. I am deeply indebted to my colleagues who participated in the field trips. I have profited much by correspondence and/or discussions with Drs. C. G. S. de Villiers, N. F. Paterson in South Africa; F. Stadmüller, in Germany; O. A. Reig, R. Casamiquela in Argentina; Z. Špinar, Czechoslovakia; A. Parnes, Z. Reis, I. Zak, A. Arad, E. Mazor, J. Lorch, M. Glikson, G. Mishnaevski, in Israel; T. H. Eaton, R. Estes, E. C. Olson, E. E. Williams in the U.S.A.; R. Oldham in Nigeria. Each contributed many constructive suggestions and criticism of the MS in whole or in part. I am particularly indebted to Dr. I. Griffiths in England for the stimulating discussions we held on various aspects of this study.

Many thanks are due to Drs. Carl Gans, R. Oldham, E. E. Williams, and Mrs. J. Lundelius for their tedious editorial contributions. Special thanks are due Mr. Eli Minkoff who gave much of his time in discussion and statistical analysis. I am grateful to the following persons for either providing or exchanging material: Drs. J. L. Perret, Cameroons; G. Reverberi, Palermo; C. A. du Toit, Stellenbosch; O. A. Reig, Buenos Aires; Ch. Stadie, Kiel; A. G. C. Grandison, British Museum (Natural History), London; R. F. Inger, Field Museum, Chicago; C. M. Bogert, R. G. Zweifel, American Museum of Natural History, New York; M. Wahrburg, Adelaide. Some of the photographs were prepared in Dr. Estes' laboratory; I am thankful to him for his courtesy and time expended.

GEOLOGY

Figs. 1, 2, 3; Pls. 1, 2

General. Makhtesh Ramon, the central breached part of the Ramon anticlinorium in the central Negev, Israel, is an erosion cirque 30 km in length with a maximum width of 8 km (Fig. 1). Its exposed rock sequence ranges in age from Middle Triassic to Cenomanian, totalling some 1200 m. The sequence consists of alternating marine and continental sediments. While the Triassic and Cenomanian strata are mainly of marine origin, the Jurassic and Lower Cretaceous beds are mostly terrestrial (Bentor and Vroman, 1951; Nevo, 1955; Shilo and Nevo, 1955; Israel Geological Society Symposium, 1963).

A generalized cross-section of the Lower Cretaceous in western Makhtesh Ramon is shown in Figure 2. The sequence, about 200 m thick, consists of "Nubian Sandstone," partly fluviatile and lacustrine, partly aeolian, with a thin marine intercalation. These Lower Cretaceous strata overlie Jurassic sediments with a pronounced angular unconformity, indicating tectonic activity at the end of the Jurassic. Extensive regression of the sea, followed by strong volcanic activity, ensued throughout the Middle East (Nevo, 1963). The resulting continental facies in the Ramon area provided the prerequisite environment for the eventual flourishing of the amphibians in early Cretaceous times.

Amphibian Hill. In Makhtesh Ramon, a regionally widespread alkaline basaltic sheet, 0–70 m thick, underlies the main Lower Cretaceous sandstones, forming a band along much of the surrounding cliffs of the cirque. The basalt sheet in western Ramon (Pl. 1 A, B) consists of two distinct flows. The amphibian zone is located between the two flows, extends over 0.25 km^2, and comprises few outcrops, the main one being 2.5 m thick and 20.0 m long (Figs. 1, 2, 3; Pl. 1 B, C). The rock consists of fine varve-like alternating dark and light laminations. The light laminations comprise silt and/or fine-grained angular quartzitic sandstone intermixed with clays, while the dark laminations are chiefly limonitic. Some laminations are continuous while others taper gradually or abruptly.

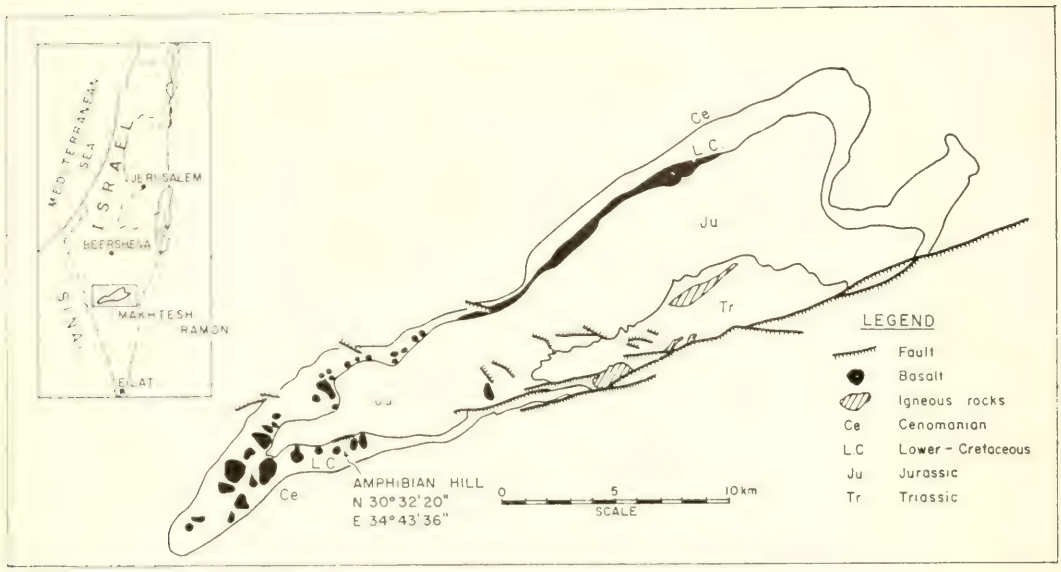


Figure 1. Location and geological map of Makhtesh Ramon.

Miniature cross bedding is visible in thin cross-sections (Pl. 1 D). The entire section contains several thousand laminations, a pair of dark and light laminae forming a "varve." The chemical analysis of the rock, in percentages, is as follows: SiO_2—54.04; Al_2O_3—16.21; TiO_2—2.71; Fe_2O_3—6.82; FeO—0.18; MnO—0.06; MgO—0.99; CaO—1.02; Na_2O—0.75; K_2O—10.00; P_2O_5—0.50; $-H_2O$—3.20; $+H_2O$—3.08; Organic material—0.08; Cl—traces; S, SO_3—0.00; CO_2—0.00; NO_3, B, F—0.00. The section contains volcanics, chiefly basalt, ash, tuffs, lapilli and bombs, indicating surrounding centers of eruption. Joints and minor faults abound in the sediment, which is diffused with limonitic red and black crusts reflecting diagenetic processes.

The numerous fossil frogs are unequally distributed throughout the deposit, yielding on the average some ten specimens per cubic meter. The number of frogs in the whole bed runs into the thousands, outnumbering all other remains. In all, 863 adult frogs and one tadpole have been collected, compared with 14 urodeles, two dinosaurian teeth, and plant remains. No other animal remains were found. While the amphibian burial assemblage was *in situ*, as indicated by the complete articulated skeletons, this was not true for all plant species, some of which were secondarily accumulated in the deposit.

Age of the amphibian zone (Fig. 2). The Lower Cretaceous sequence unconformably overlies strata of Jurassic age (Nevo, 1955), and underlies those of Cenomanian age (Bentor and Vroman, 1951); for a list of Jurassic and Cenomanian fossils refer to Figure 2. Abundant plant remains occur throughout the sequence (Pl. 2); some indicate a general Lower Cretaceous age, whereas others point definitely to a pre-Albian, probably Neocomian age. *Weichselia reticulata* Stokes and Webb occurs throughout most of the sequence (Shilo and Nevo, 1955), indicating a Lower Cretaceous age (Teixeira, 1948). Figure 2 lists the plant assemblage associated with the fossil frogs (described by Lorch, 1963). The species *Brachyphyllum obesum* Heer, *Cladophlebis* cf. *browniana* Dunker, *Cladophlebis* cf. *dunkeri*, and *Desmiophyllum zeillerianum* are common in the Wealden, indicating a pre-Albian, probably a Neocomian age (Teixeira, 1948). A second

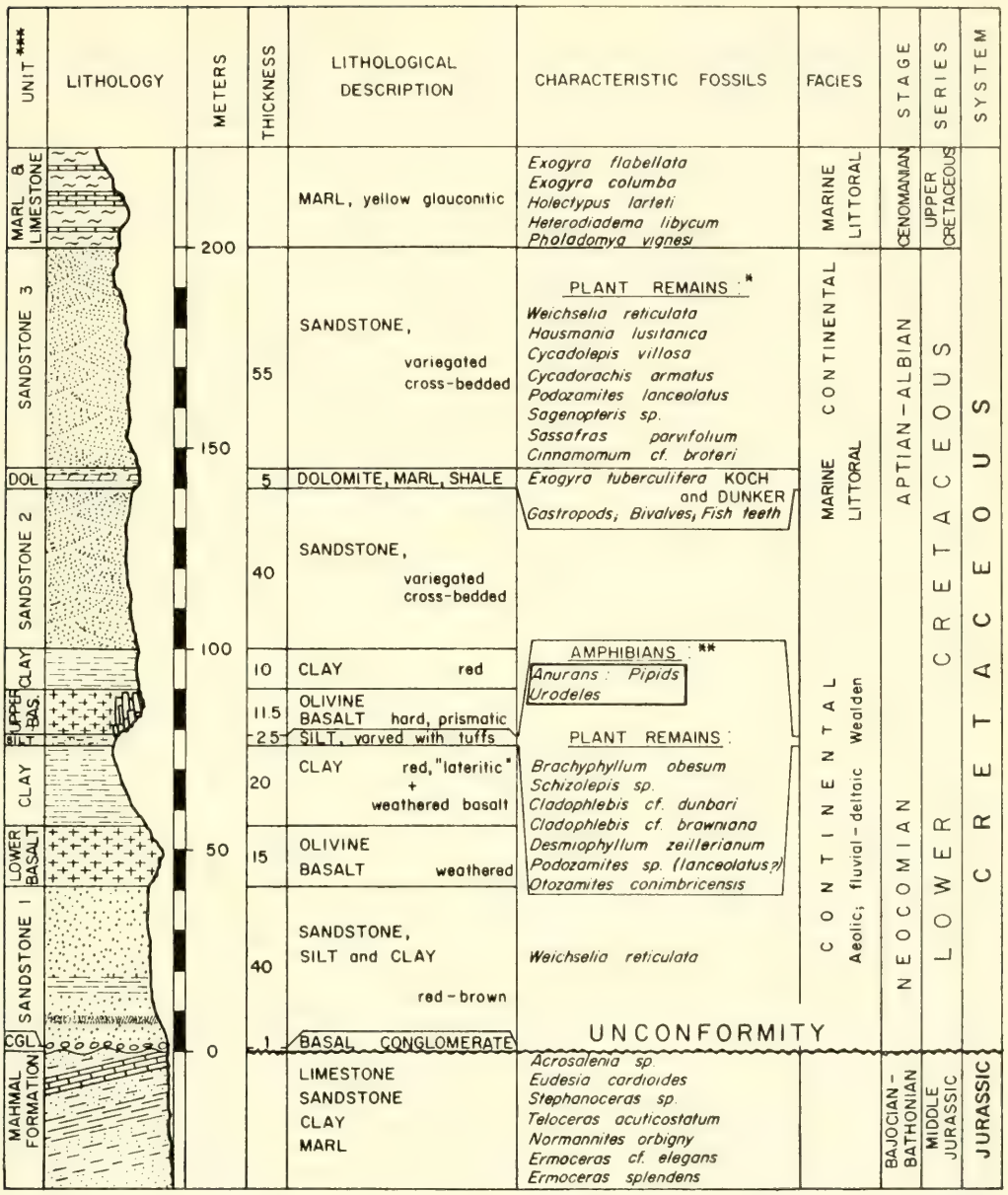


Figure 2. Generalized columnar secton, Lower Cretaceous western Makhtesh Ramon.

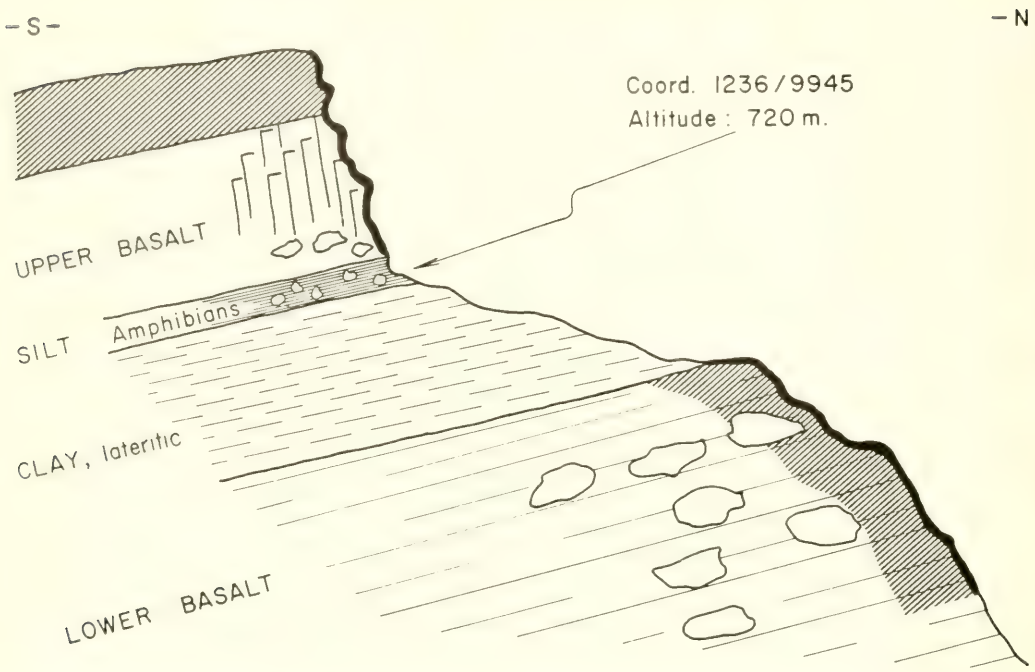


Figure 3. Geological cross section (diagrammatic) through Amphibian Hill, Makhtesh Ramon (Longitude: E 34° 43′ 36″; Latitude: N 30° 32′ 20″).

plant assemblage, some 100 m above the former, in which *Weichselia reticulata* is associated with other filicales, gymnosperms, and dicotyledons, has been assigned an Albian age (Lorch, 1963). A further confirmation of the pre-Albian, probably Neocomian, age of the amphibian bed is furnished by the marine intercalation of the Lower Cretaceous, situated some 75 m above the amphibian zone (Fig. 2). The intercalation contains various ostracids, among them *Exogyra tuberculifera* Koch and Dunker, which ranges from the Valanginian to the Aptian, and is common in the Neocomian of Europe (Woods, 1912). Its occurrence indicates, at the most, an Aptian age for the marine intercalation (Mishnaevski, personal communication). In any event, since the amphibians occur near the bottom of the section, they belong to the lower part of the Lower Cretaceous.

No foraminifers or ostracods were found in the marine intercalation. The low concentrations as well as the unfavorable ratios in which Ru, Sr, K and Ar occur in the lower and upper basalts make these rocks extremely difficult for absolute age determinations (Mazor, personal communication).

PALEOECOLOGY

Climate. Several lines of evidence suggest a humid-warm climate in the Ramon area during Lower Cretaceous times. The first is the nature of the fossil frogs and the dinosaurian teeth. The frogs belong to the Pipidae, a purely aquatic frog family, comprising three genera and fifteen species, restricted today to tropical and subtropical regions of South America and Africa. The worldwide distribution of dinosaurian faunas in early Cretaceous times also implies tropical or subtropical climates (Colbert, 1964). The second is the formation of red lateritic clayey soil during the volcanic Lower Cretaceous basalt phase, par-

ticularly following the lower basalt flow and preceding the lake period. The third is the abundance of fluvio-deltaic sediments abounding with kaolinitic clays and rich in warm-type flora in early Cretaceous times. Finally, Lowenstam (1964), using Urey's oxygen isotope method, estimated average temperatures of 24° C for marine waters of Albian times at 30° N, as compared with 21° C at present.

Environment. The following habitat picture has been inferred from the geological, chemical, climatic, and biological data presented above. The evidence suggests that the frogs inhabited a small, shallow, freshwater lake having an outlet. A rich littoral vegetation bordered the lake: Bennettitales similar to *Otozamites*, conifers, including *Schizolepis*, *Brachyphyllum* and *Podozamites*, and ferns, including species of *Cladophlebis*. *Weichselia reticulata* predominated farther from the lake in the sandy habitats. The topography was low, composed of sandstone hills and scattered volcanoes. The lake lasted several thousand years at the most, and was apparently continuous throughout that time until dried up by the second or upper lava flow. The surrounding volcanoes erupted recurrently, pouring a part of their wastes into the lake, polluting the water and causing irregular mass mortalities among the frogs. Sedimentation in the lake was quiet, periodic, mostly in standing or very slowly flowing water.

The lake waters were warm, soft, possibly acidic, and abounded with decaying plants. The oxygen content was low with a reducing bottom. The latter resulted from a high H_2S content, typical of freshwater lakes in tropical regions and of volcanic environments. The lake bottom was presumably barren of all living organisms except anaerobic bacteria, thus providing ideal conditions for frog preservation, resulting in complete intact skeletons, undisturbed by any scavengers. The lake was thus oligotrophic and probably had a low productivity caused by the low content of nitrates, phosphates, and carbonates, high stagnation, poor aeration and not infrequent ash falls from the surrounding volcanoes. In all, the fauna was very poor in species, apparently reflecting the general unfavorable condition of the lake water. The food sources of the frogs and urodeles remain a riddle.

MATERIALS AND METHODS

Field work. This study is based on 863 postmetamorphic fossil frogs of which 344 were studied in detail. All the material was collected by the author and many colleagues during the period 1954–1962 from the same outcrop in western Makhtesh Ramon, Israel (Figs. 1, 2, 3; Pl. 1).

The collecting consisted of recovering slabs of rock, mainly by hammer and chisel. Only once were explosives used to get rid of the basaltic overburden. The original layering greatly facilitated the recovery of slabs that were later cleaved by light hammer strokes along the fine varves in order to reveal the frogs. These were easily detected by following the limonite-encrusted varves. Cleaving was done either in the field or in the laboratory. After cleaving, portions of the skeleton remained on both sides of the slabs as part and counterpart. The extreme fragility of both matrix and fossils required efficient packing and careful transporation from field to laboratory.

Preservation of fossils. Most of the material was preserved as complete skeletons, with only a few single bones or masses of disarticulated elements. The method of recovery of the material from the deposit and the extensive jointing within the sediment resulted in a high frequency of fractures. Preservation varies from excellent to poor. About 10 per cent of the specimens are mere imprints in the silt and therefore unworkable; the rest are preserved as either limonitic original bones or colored imprints. The skeletons were replaced, partially or entirely, by ferric oxides. The finer the sediment the better was the preservation. Preparation was hampered by the fragility

Table 1. Comparative Recent and Fossil Material Studied

Family	Species	Provenance	No. of Specimens
RECENT			
Ascaphidae	*Ascaphus truei*	Washington (state), USA	3
,,	*Leiopelma hochstetteri*	New Zealand	1
Pipidae	*Pipa pipa*	Brazil, British Guiana	3
,,	*Hemipipa carvalhoi*	Brazil	1
,,	*Hymenochirus boettgeri*	Cameroons	10
,,	*Xenopus laevis*	Stellenbosch, South Africa	5 adults 5 larvae
,,	*Xenopus tropicalis*	Niapu, Congo	3
,,	*Xenopus gilli*	South Africa	3
,,	*Xenopus mulleri*	Farjade, Congo	3
Discoglossidae	*Discoglossus pictus*	Sicily	10
,,	*Discoglossus nigriventer*	Israel	1
,,	*Bombina bombina*	Italy	2
,,	*Bombina variegata*	Italy	10
,,	*Alytes obstetricans*	Europe, locality unknown	2
,,	*Alytes cisternasii*	Spain	1
Rhinophrynidae	*Rhinophrynus dorsalis*	Mexico	3
Pelobatidae	*Pelobates syriacus*	Haifa, Israel	3
,,	*Pelobates fuscus*	Germany	2
,,	*Scaphiopus holbrooki*	Texas, USA	2
,,	*Scaphiopus couchi*	Texas, USA	2
,,	*Scaphiopus hammondi*	Arizona, USA	2
,,	*Megophrys hasselti*	Philippine Islands	2
Leptodactylidae	*Rhinoderma darwini*	Chile	1
,,	*Leptodactylus ocellatus*	Brazil	2
,,	*Leptodactylus bufonius*	Argentina	4
Bufonidae	*Bufo bufo*	Germany	2
,,	*Bufo viridis*	Saar, Israel	15
,,	*Bufo typhonius*	Venezuela	4
Pseudidae	*Eleutherodactylus nasutus*	Brazil	1
Hylidae	*Hyla arborea*	Saar, Israel	5
Ranidae	*Rana ridibunda*	Oranim, Israel	10
FOSSIL			
Pipidae	*Saltenia ibanezi*	Cretaceous, Argentina	5
	Hekatobatrachus grandipes	Miocene, Czechoslovakia	2

of the skeletons. During fossilization there was crushing and flattening of the skeletons, thus eliminating some structural details; consequently, the description is composite.

Laboratory work. The material was examined under binocular microscope while immersed in xylol to disclose features not observable in the dry specimens. Some 200 specimens in xylol were photographed on Kodak microfilm. Line drawings were made by tracing projected negatives.

The fossil material was compared with skeletons of living frogs, utilizing X-ray photographs (particularly for studying variation [Vose, 1958]), alizarine-red S transparencies (Williams, 1941), and dry skeletons (Sanders, 1953). Table 1 lists the skeletons of Recent species examined.

Statistics. Vernier caliper measurements were made to 0.1 mm on 248 fossil skeletons under the binocular dissecting microscope; 28 variates were recorded. No specimen was sufficiently complete to permit all 28 measurements. The data were analyzed using four IBM 7090/7094 computer programs for generating new variables, univariate statistics, scatter diagrams and

histograms, and computing Mahalanobis distance among the three species. (The detailed biometric results and a study of variation will be reported in a separate paper.)

Location of material. The collection is deposited in the Department of Zoology, Hebrew University of Jerusalem (HUJZ). Of the 863 specimens in the collection, only 344 were numbered systematically. The prefix F runs before the number, whereas suffix a or b runs after it, designating part and counterpart whenever present; e.g. F 241 a and F 241 b.

SYSTEMATIC DESCRIPTIONS

Family PIPIDAE

THORACILIACUS gen. nov.

Type species. *Thoraciliacus rostriceps* sp. nov.

Diagnosis. A pipid closely related to *Eoxenopoides reuningi*, *Shelania pasquali*, and *Saltenia ibañezi* (see Table 8), but differing from these in having a free monocondylar sacro-urostylar articulation and one or more discrete postsacral vertebrae; in the absence of a suture between the frontoparietals; in the prominent rostrum; in the maxillae and premaxillae bearing teeth; in the sword-like parasphenoid; in the triangular transverse processes of presacrals 6–8; and in the articulation of tips of the ilia with the ribs.

Generic description. An anuran of pipid affinity. *Vertebral column*: Eight opisthocoelous, ectochordal presacral vertebrae; sacrum consisting of the 9th opisthocoelous vertebra with strongly expanded diapophyses; usually one postsacral vertebra; four pairs of free ribs attached to presacrals 2–5; diapophyses of presacrals 6–8 triangular and anteriorly directed; urostyle free from sacrum, with a single condyle. *Pectoral girdle*: Arciferous; clavicles large, strongly arched, meeting anteriorly, overlying the scapula posteriorly; coracoids strongly diverging from clavicles, straight shafts expanded at both ends much more mesially where they meet; scapula small, triangular, uncleft; suprascapula large, elongated, feebly ossified, supporting a large, strongly ossified V-shaped cleithrum; no sternum and episternum. *Skull*: Large, broader than long, quadrate region posteriorly situated; nasals large, forming a prominent anteriorly rounded rostrum; frontoparietals azygous, vase-shaped, large, strongly ossified; premaxillae with 10 teeth; maxillae with 35 teeth, tapering posteriorly without any contact with the quadrate [an incomplete maxillary arcade]; squamosals slender, small. No quadratojugals, palatines or mentomandibulars; vomers small, paired, anteriorly triradiate; pterygoids large with anteriorly thinning arcuate extensions; quadrate subquadrangular, well ossified; parasphenoid sword-like, its anterior tapering blade protruding in front of the maxillae, its posterior third wider, broadening into short lateral processes; sphenethmoid single, ossified, protruding anteriorly between nasals; otic capsules extensive, almost spherical; plectrum of columella outstanding; lower jaw comprises slender edentulous dentary, and prominent prearticular. *Pelvic girdle*: Large; ilia long, extending anteriorly beyond sacral diapophyses, their tips articulating with ribs 3 and/or 4; pubis strongly ossified; ischium long, ossified; no epipubis. *Forelimb*: Humerus straight, mostly smooth, with a small proximal ventral crest, proximally expanded, distally having a well-developed spherical capitate eminence; radioulna single, flat, expanded at both ends, with a prominent olecranon and a longitudinal intermedial groove; nine carpals; four subequal fingers with very long slender metacarpals and 2, 2, 3, 3 phalanges, the terminals of which are pointed; no prepollex. *Hindlimb*: Femur faintly S-shaped with a short femoral crest; tibiofibula single, slightly shorter than femur, with a longitudinal intermedial groove; tibiale-fibulare elongated, fused at both ends; five distal tarsals; no prehallux phalanges; five toes with long metatarsals and 2, 2, 3, 4, 3 phalanges, the terminals of which are

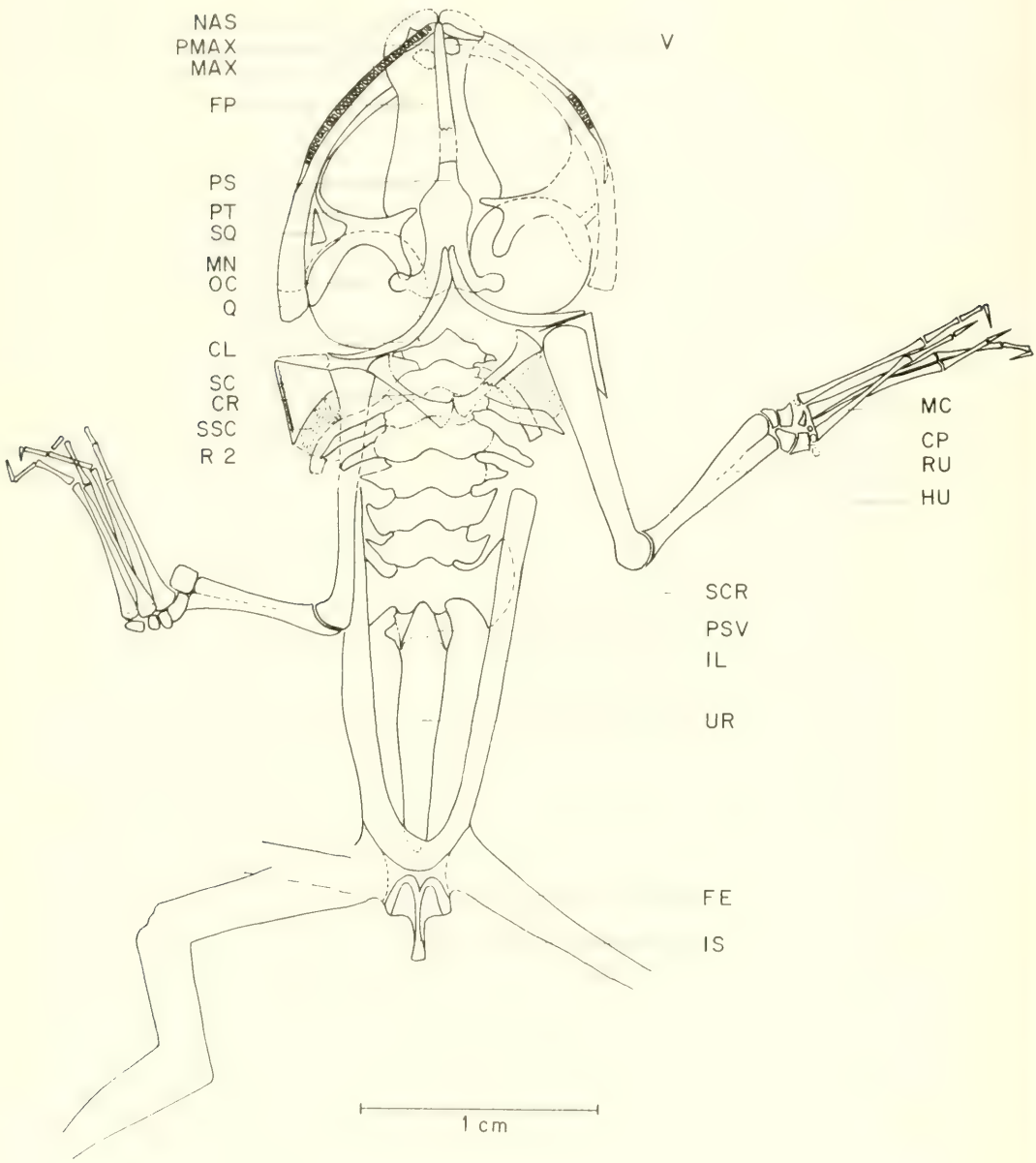


Figure 4. *Thoraciliacus rostriceps*, HUJZ, F 93, type specimen, ventral aspect. Abbreviatons: CL-clavicle; CP-carpal; CR-coracoid; FE-femur; FP-frontoparietals; HU-humerus; IL-ilum; IS-ischium; MAX-maxilla; MC-metacarpal; MN-mandible; NAS-nasal; OC-otic capsule; PMAX-premaxilla; PS-parasphenoid; PSV-postsacral vertebra; PT-pterygoid; Q-quadrate; R2-rib 2; RU-radioulna; SC-scapula; SCR-sacrum; SQ-squamosal; SSC-suprascapula; UR-urostyle; V-vomer.

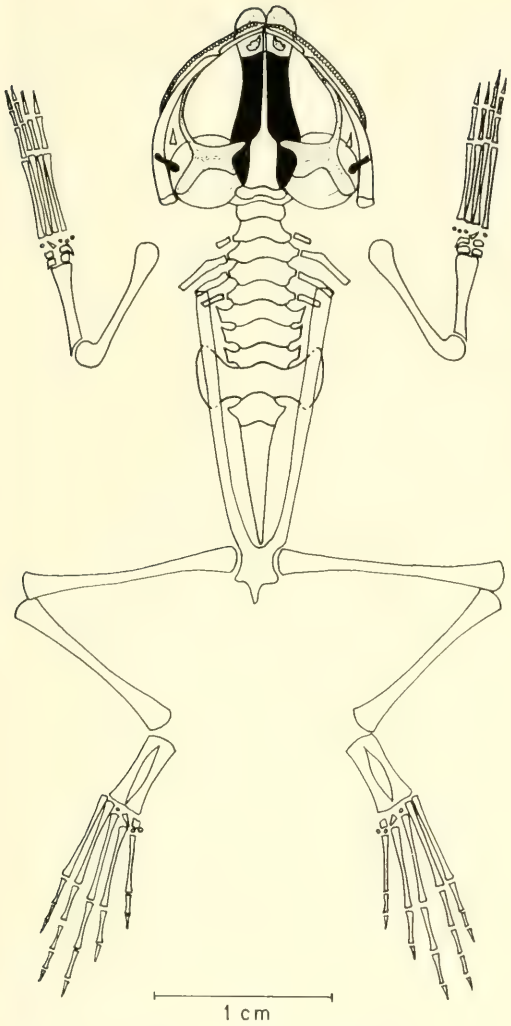


Figure 5. *Thoraciliacus rostriceps*, reconstruction.

pointed; all epiphyses of long bones in both fore- and hindlimb are well ossified.

Thoraciliacus rostriceps sp. nov.

Figs. 4, 5, 10–13; Pls. 3–6; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology No. F 93, nearly complete skeleton lacking most of the hindlimbs (Pl. 3 A).

Hypodigm. Type and specimens F 1–148, 210–240, 247–250, 253.

Horizon and locality. Silt unit between lower and upper basalts, Lower Cretaceous (Fig. 2). Coordinates 1236/9945 (Israel Topographical Map); latitude: 30° 32′ 20″ N; longitude: 34° 43′ 36″ E; western Makhtesh Ramon, Israel; collected by Eviatar Nevo in 1954.

Specific diagnosis. Same as for genus; sole known species of the genus.

Description of the type material. A well preserved small frog represented by the original bones heavily impregnated by dark limonitic ferric oxides; distinctly flattened as a result of fossilization. Right hindlimb crushed proximally, and both hindlimbs lacking distally; in ventral aspect. Absent parts are described from F 41 a (Pl. 6 E).

General description. Skull (Fig. 10 C). The skull is large, wide and flat. It is somewhat broader than long, slightly longer than the eight presacral vertebrae. The maxillary arcade is incomplete. A prominent rounded rostrum projects beyond the mouth. The quadrate region is posteriorly situated. The nasals are large, broad and kidney-shaped, rounded anteriorly and forming the rostrum (Pl. 6 D); they meet anteromesially and diverge posteriorly to expose the central extension of the sphenethmoid; dorsally they have fanlike striations.

The frontoparietals form a broad azygous slab, strongly and totally ossified; they dominate the dorsal aspect of the skull and have a vaselike shape; anteriorly they contact the sphenethmoid; posteriorly they partly overlap the synotic region; the lateral portions are anteriorly concave, posteriorly convex, and exhibit slightly thickened supraorbital ridges. The premaxillae are overlain by the nasals and have a small triangular facial process; each premaxilla carries 10 teeth, mostly recognizable by their sockets. The maxillae are gently curved, tapering posteriorly to end in front of the posterior border of the orbit, or just at this level; since the quadratojugals are absent and no contact exists with the quadrate, a considerable gap obtains between

the maxilla and quadrate, resulting in an incomplete maxillary arcade. A maxillary frontal process forks anteromesially, ending freely. Each maxilla carries 35 teeth evenly spaced throughout its entire length; mostly the teeth are recognizable through their sockets, but in F 63 conical little teeth are preserved.

The squamosals are small, slender, rod-like or triangular bones, apposing the otic capsules. The quadratojugals and palatines are absent. The vomers are small, paired, anteriorly triradiate, the median projection being the longest; they are only rarely preserved (F 36, 85, 93, 112, 293). The pterygoids are well developed, overlapping the anterolateral portions of the otic capsules. Their broad root is triradiate; the anteromesial arm is short, contacting the broader part of the parasphenoid; the posterolateral arm is the longest of the basal processes and contacts the quadrate; the broad root extends anterolaterally to meet the maxilla as a long, anteriorly thinning arcuate extension. The quadrate is subquadrangular, small, well ossified and only rarely visible (but can be seen in F 47, 52, 112, 120, 321). The parasphenoid is sword-like and prominent along the ventral aspect of the skull from the mid-otic capsules, posteriorly, to near the edge of the rostrum in front of the maxillary arcade; its anterior two-thirds consists of a narrow tapering rod, the "blade," while the posterior third is much wider and broadens into short lateral processes (Pls. 4 B, 6 C); the bone is rarely preserved complete (it is complete in F 20, 39, 93, 270, 309, 310), but is frequently represented just by its anterior acuminate portion. The sphenethmoid is single, well ossified, and fills the gap between the frontoparietals and nasals. Posteriorly it is emarginated; anteriorly it protrudes between the nasals.

The otic capsules are formed by the strongly ossified, very large, spherical prootics, dominating the posterior skull and situated mainly anterior to the quadrate; they are partly overlapped dorsomesially by the posterior portion of the frontoparietals, while ventromesially they are bordered by the exoccipitals which form the occipital condyles. The position of the semicircular canals shows clearly inside the capsules in several specimens (e.g., in F 60, 83, 84, 109, 128, 135, 138, 252). The plectrum of columella is preserved in 20 specimens. It is a small but well-ossified rod, 2.15 mm long and 0.4 mm wide, slightly arched, with a little swollen base abutting upon the fenestra ovalis proximally, ending freely distally.

The lower jaw consists of the dentary and prearticular only, the mentomandibulars being absent. The dentary is slender, edentulous, and articulates with the outer side of the prearticular, terminating close to the posterior limit of the maxilla. The prearticular is very large, strongly ossified, forming the principal element of the lower jaw; it has a prominent coronoid process in close apposition to the pterygoid, articulating post-otically with the quadrate.

Vertebral column (Fig. 11 C). There are usually eight presacral vertebrae; no fusions occur between successive vertebrae throughout the column. The presacrals are similar in shape. The vertebrae are flat and broader than long, with flat neural arches and short neural spines. The latter do not imbricate and, in several cases, the vertebral centra are exposed in dorsal aspect. The centra are opisthocoelous and ectochordal, consisting of an ossified cylinder enclosing a hollow tube reminiscent of a persistent notochord. (This is clearly shown by the optical section through a transparent vertebra immersed in xylol, which shows an hour-glass effect; see F 36 on Fig. 15 and F 40 on Pl. 4 B.) The atlas is usually free of diapophyses. Presacrals 2–5 possess horizontally directed short transverse processes, articulating with the corresponding ribs; the transverse processes of presacrals 6–8 are highly diagnostic, being triangular, sharply pointed, and anteriorly directed.

Four pairs of free ribs are confined to

the 2nd, 3rd, 4th, and 5th presacrals, hereafter referred to as ribs 1, 2, 3, 4, the first rib arising from the transverse processes of the second vertebra, etc. (Pl. 4 B). The first rib is the smallest, mostly directed posterolaterally. The second rib is generally the largest, usually arcuate, and posterolaterally directed. A few specimens show faintly expanded impressions on tips of second ribs, probably indicating a cartilaginous link between ribs 2 and 3. The third rib is also large but usually smaller than the second. It is bent posterolaterally, nearly parallel to the second rib. The fourth rib is smaller than the preceding two, usually exceeding in length only the first rib. It is mostly posterolaterally directed, but occasionally is horizontal or even pointed anterolaterally. Partial fusions of ribs to their corresponding transverse processes are not rare. This is particularly true for the first and fourth ribs. Apart from a few inconclusive cases, no uncinate processes were found.

The sacrum consists of the ninth opisthocoelous vertebra and has strongly expanded diapophyses. The urostyle is free from the sacrum, articulating with the latter by a single condyle. It tapers posteriorly, reaching, and sometimes overlying, the pubis. The urostyle has as a rule one proximal vertebra.

Pectoral girdle (Fig. 12 C; Pls. 5 C, 6 C, F). The pectoral girdle is inferred to be arciferal on the evidence of the strongly diverging coracoids and clavicles. The clavicles are very large, strongly arched, and strongly ossified; their anteriorly expanded ends meet midventrally, reaching the anterior portion of the otic capsules. The coracoids are posteriorly directed, strongly diverging from the anteriorly directed clavicles; they are well ossified, stout straight shafts, expanded strongly at both ends, but more so posteriorly, where they meet. The scapula is a small, triangular, strongly ossified bone, having a posterior distal spur and a diagonal distal border; the proximal margin is normally uncleft, lacking the notch separating the acromial from the glenoidal process (Pl. 6 A, C). The suprascapula is a weakly ossified large petaloid blade, posteriorly elongated and rounded; it reaches the level of the 4th presacral, overlying the second and third ribs. The cleithrum is a large, V-shaped, strongly ossified bone, investing the anterior and lateral margins of the suprascapula; it has two osseous prongs, the posterior being stouter and shorter than the anterior; it was preserved in 39 specimens. No traces of sternum, episternum, coracoidal cartilages, or epicoracoidal horns were found.

Pelvic girdle (Fig. 11 C; Pl. 6 A, E). The most remarkable feature of the pelvis is the anterior extension of the tips of the long ilia, which make contact with the third and/or fourth ribs, rarely ending freely. Consequently, the ilia articulate with two or three extensions of the column, thus tending to bind together vertebrae four through nine. A functional synsacrum is thus formed, but no fusion of vertebrae occurs. (In this genus the tips of the ilia thus make an iliocostal contact, in addition to the contact effected with the sacral diapophyses at the middle or anterior portions of the ilia—"medioiliac" contact; these two articulations contrast with the normal single anuran "acroiliac" articulation—tip of ilium forming the contact with the sacral diapophyses. Hereafter, the *Thoraciliacus* condition will be consistently distinguished as iliocostal or medioiliac articulation from the acroiliac or more usual anuran articulation.) The ilia are simple and smooth in most cases, but are variable in form and divergence; mostly they are straight rods, but some are slightly convex externally either near the acetabulum or throughout their length; others are asymmetric. The ilia are longer than the vertebral column plus the sacrum. The pubis is strongly ossified. An important feature of the pelvis is the relatively great posterior extent of the ischium in most specimens. No traces of epipubis were found.

Forelimb (Fig. 13 C). The humerus is

straight, expanded at both ends but distinctly more so towards the proximal end where it attains its maximal diameter, being capped by the well-ossified humeral cap; distally, it has a well-ossified, developed, spherical capitate eminence; the lateral epicondyle is very weakly developed, while the medial one is mildly so; the cubital ventral fossa is a small triangular pit; the shaft is distinctly smooth and crestless apart from the very short proximal ventral crest. No differences could be associated with sex. The radioulna is shorter than the humerus, single, flat and expanded at both ends, more so distally. Its dual origin is disclosed both by the intermedial groove extending over the distal two-thirds of its length, and by the presence of two distinct bones at the distal end; proximally, the olecranon process is prominent; no bony crests. There are nine carpals arranged in three rows; these are, following the nomenclature of Howes and Ridewood (1888): the radiale and ulnare in contact with the radioulna, two centrales in the second row, and five distal carpals in the third row. The radiale, ulnare, and centrales are big, subquadrangular, forming a characteristic tetrad; the inner centrale has a diagnostic posterior spur; all four are smooth dorsally but exhibit irregularities on their volar surface. The five distal carpals involve four small bones corresponding each to its respective metacarpal, and a small prepollex carpal discerned between the second carpal and inner centrale. The four distal carpals diminish in size in the following order: 4-2-5-3. Carpals 2, 3, 5, as well as the prepollex carpal, are small spheres, whereas carpal 4 has a diagnostic triangular shape. When the prepollex carpal is included, the total number of free carpals is nine. No phalangeal elements are associated with the prepollex carpal. No sex differences nor any fusions of carpals were discerned. Mostly the carpals are either missing or obscure; in only 28 out of 281 cases were they analyzable. This fate is shared also by the prepollex carpal because of its smallness and external position: it was eventually found in just four out of the above 28 specimens. (It is well preserved in F 297.) There are four elongated subequal fingers and 2, 2, 3, 3 phalanges, the terminals being pointed. The remarkable feature of the manus is the very long and slender metacarpals resulting in surprisingly long fingers.

Hindlimb (Fig. 13 C; Pls. 5 B, 6 E). The femur is strong, long, and shows a slight sigmoid curvature. It is expanded towards both ends where it has well-ossified epiphyses. The proximal femoral head is elliptical, fitting into the acetabulum of the same shape. Proximally, there rises a short, rather low femoral crest. The tibiofibula is even stronger, but slightly shorter, than the femur. It is approximately straight, being also expanded towards both ends, where it has well-ossified epiphyses. Its dual nature is disclosed throughout by the distinct intermedial groove. The tarsus consists of the characteristic tibiale-fibulare and five free distal tarsals. The tibiale and fibulare are elongated, broadening medially towards both ends where they meet, leaving a conspicuous interosseous space throughout their length. The tibiale is more slender than the fibulare. When seen entirely separated, as in F 36, they certainly suffered dislocation, suggesting a weak fusion. The distal tarsals are located between the inner three metatarsals and the tibiale, whereas the two outer metatarsals contact the fibulare leaving no space for any additional distal tarsals. The five distal tarsals involve a large centrale (= naviculare) attached to the tibiale, a prehallux tarsal in contact with the centrale, and a series of three smaller tarsals each corresponding to the three inner metatarsals. While both the first and third distals are small and round, the second is diagnostically large and triangular. There are five toes with strikingly elongated metatarsals, and 2, 2, 3, 4, 3 phalanges, the terminals being pointed. No phalanges are associated with the prehallux tarsal. The toes are unequal

in length: The third is the largest and usually exceeds the fourth in length, but equals it in some cases; the second equals the fifth, the first toe being the shortest.

CORDICEPHALUS gen. nov.

Type species. *Cordicephalus gracilis*, sp. nov.

Diagnosis. A small anuran of pipid affinity, similar in most basic characteristics to *Thoraciliacus rostriceps*, from which it differs primarily in skull and pelvis (Figs. 10, 11, 13 and Tables 6, 7). The following are the features characterizing *Cordicephalus* as contrasted with *Thoraciliacus*: general slenderness of the entire skeleton; articulation of pelvic girdle acroiliac, with the tips of ilia articulating with sacral diapophyses; ilia diverging to form a triangle; ischium medium in length; skull heart-shaped (hence the generic name); no prominent rostrum; quadrate anteriorly placed; anterior extensions of pterygoid and mandible curved; otic capsules ellipsoidal or rectangular; third rib longer than second; transverse processes of presacrals 7 and 8 arcuate; one or two postsacral vertebrae; longer humerus and radioulna. See Table 4 for statistically significant differences between *Cordicephalus* and *Thoraciliacus*.

Cordicephalus gracilis sp. nov.

Figs. 6, 7, 10–13; Pls. 7–9; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology No. F 165, nearly complete skeleton, lacking some portions of the pectoral girdle.

Hypodigm. Type and specimens F 149, 151, 153–155, 157–166, 168–170, 172, 174–187, 190–191, 197–209.

Horizon and locality. Same as for *Thoraciliacus rostriceps*.

Specific diagnosis. A very small *Cordicephalus*; no rostrum; nasals in form of crescentic bars; wide rear portion of parasphenoid having lateral processes both anteriorly and posteriorly; sphenethmoid with long triangular anterior prolongation; otic capsules ellipsoidal; ribs medium to long; sacral diapophyses broadening gradually distally; mostly two postsacrals; ilia diverge by about 45°; scapula uncleft; suprascapula triangular.

Description of type material. A well-preserved small and slender frog represented by original bones, heavily impregnated by dark limonitic ferric oxides. Slightly flattened due to fossilization.

Skull (Fig. 10 B). The skull is slightly broader than long, with a heart-like shape. The maxillary arcade is incomplete, and there is no rostrum. The quadrate region is anteriorly situated. The nasals overlie the premaxillae, in line with the maxillary arch, and form a rounded anterior contour. They are well-developed, elongated, crescentic bars, meeting mesially above the anterior arrow-like extension of the sphenethmoid and fitting closely into the anterior concave margins of the latter. The frontoparietals form an azygous, vaselike, strongly and totally ossified slab, approximating in shape, relations and contacts that of *T. rostriceps*. No median suture or pineal foramen were found in ten specimens examined for these features. The premaxillae and maxillae follow closely the *Thoraciliacus* pattern. Both bones are dentigerous but have smaller numbers of teeth than in the latter genus; about 25 in the maxilla and 8 in the premaxilla. The maxillary arcade is incomplete due to the absence of quadratojugals. The squamosals are small, slender splints, rarely preserved. There are no quadratojugals and no palatines. The vomers are apparently disclosed in only two cases (F 168, 176), each being triangular, forming with its partner a rhomboid structure near the anterior tip of the parasphenoid. The pterygoids are well developed, characterized by their curved anterior extension. The quadrate is a subquadrangular, well-ossified bone. The parasphenoid is sword-like, as in *Thoraciliacus*, differing from the latter in having horn-like projections at the base of the blade. In most cases only the blade is preserved. The sphenethmoid is single, well ossified; its

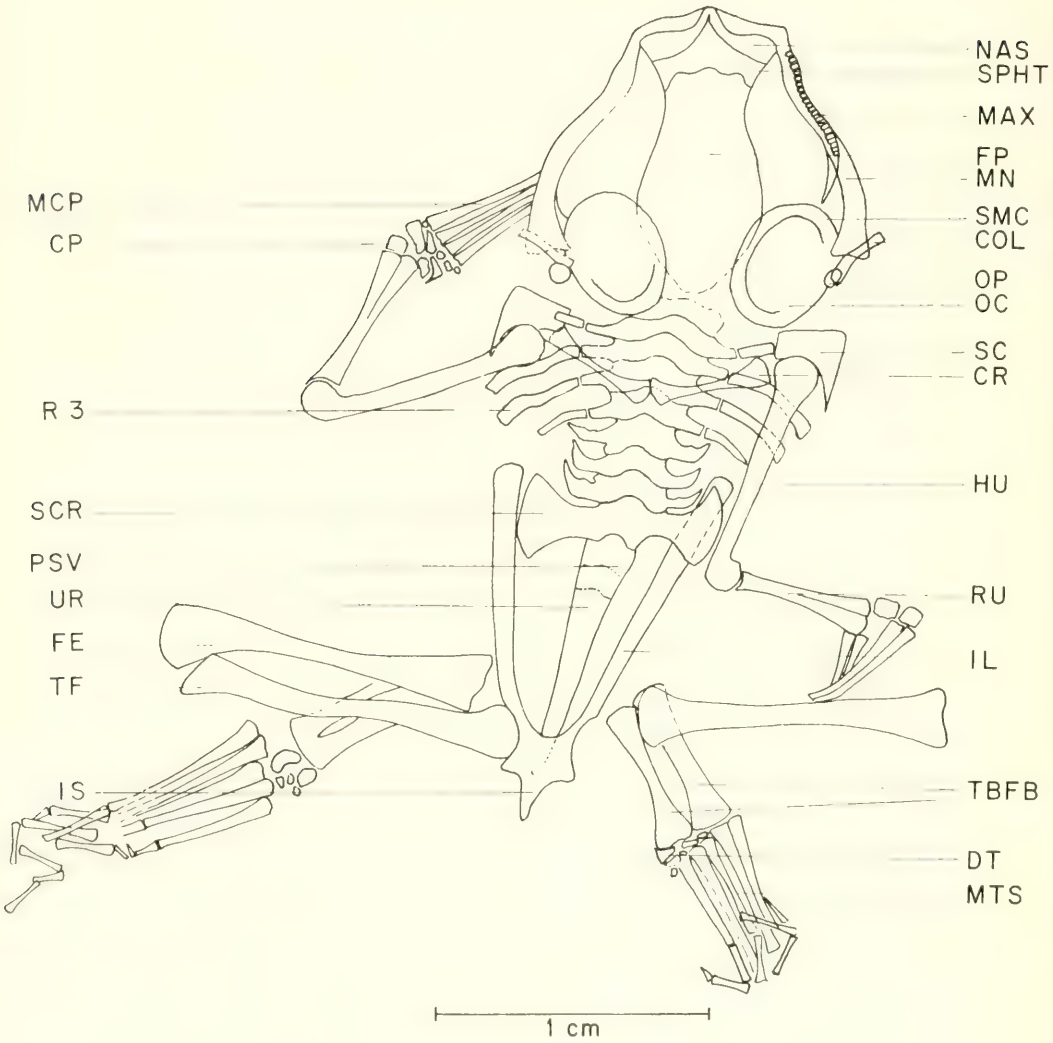


Figure 6. *Cordicephalus gracilis*, HUJZ, F 165, type specimen, dorsal aspect. Abbrevations: COL-columella; CP-carpal; CR-coracoid; DT-distal tarsal; FE-femur; FP-frontoparietals; HU-humerus; IL-ilium; IS-ischium; MAX-maxilla; MCP-metacarpal; MN-mandible; MTS-metatarsal; NAS-nasal; OC-otic capsule; OP-operculum; PSV-postsacral vertebra; R3-rib 3; RU-radioulna; SC-scapula; SCR-sacrum; SMC-semicircular canal; SPHT-sphenethmoid; TF-tibiofibula; TBFB-tibiale-fibulare; UR urostyle.

head projects distinctly to the front, much more than in *Thoraciliacus*. The otic capsules resemble those of *Thoraciliacus* in being extensive and intensely ossified, but differ in being obliquely ellipsoidal. The longitudinal axes of the two capsules form a right angle. Within the capsules the position of the semicircular canals shows clearly. The most remarkable feature associated with the capsules is the plectrum of the columella, seen in 8 specimens. It closely resembles the columella of *Thoraciliacus*, both in shape and size, but differs in its association with a small spherical ossified operculum, posterior to and abutting upon the fenestra ovalis (Pl. 9 D). It is

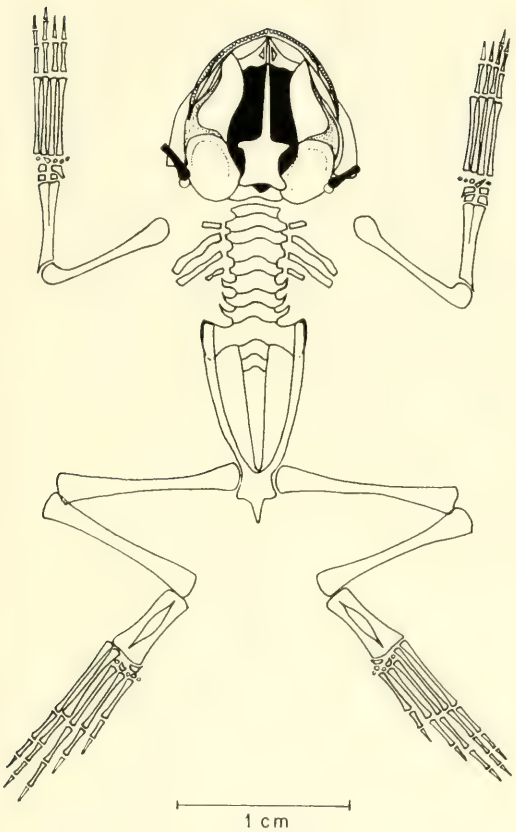


Figure 7. *Cordicephalus gracilis*, reconstruction.

probable that the swollen base of the plectrum represents the internal part of the columella, which was possibly ossified. The plectrum is 2.1 mm long and 0.3 mm wide. The lower jaw is arcuate, giving the skull, together with the anterior curved prolongation of the pterygoid, its heart-shaped form. It articulates pre-otically with the quadrate, thus differing from the post-otic condition of *Thoraciliacus*.

Vertebral column (Fig. 11 B). There are eight presacral vertebrae displaying no fusion. All are similar in shape, flat, broader than long. The neural arches are low; the neural spines short, non-imbricating, occasionally exposing the centra. The centrum is invariably opisthocoelous. The atlas is free of appendages. Presacrals two through five have relatively short transverse processes; those of presacral six resemble a more delicate version of the corresponding processes of *Thoraciliacus*. The transverse processes of presacrals seven and eight are highly diagnostic, differing basically from those of *Thoraciliacus*; they are arcuate as contrasted with the triangular ones of the latter, and anteriorly directed. Four pairs of slender ribs are confined to the second, third, fourth, and fifth presacrals, hereafter referred to as ribs 1, 2, 3, 4, the first arising from the transverse processes of the second presacral, etc. (Pls. 8 B, 9 G). The first rib is the smallest, directed anterolaterally. The third rib is the longest, followed in length by the second and fourth ribs, differing in this respect from *Thoraciliacus*, the second rib of which is the longest. The second through fourth ribs are posterolaterally directed, none ever having any contact with the tips of the ilia.

The sacrum consists of the ninth opisthocoelous vertebra, which has expanded diapophyses. The urostyle is free from the sacrum, articulating with the latter by a single condyle. It has in most cases a swollen base, tapering chiefly in its posterior two-thirds. Careful analysis, in xylol, disclosed in its proximal portion, otherwise obscure centra mostly lacking diapophyses; two postsacrals predominate.

Pectoral girdle (Fig. 12 B; Pl. 9 A, B). The pectoral girdle is arciferal, a delicate replica of the *Thoraciliacus* girdle and exhibiting only a few small differences from the latter. The clavicles are strongly arched and markedly diverge from the posteromesially directed coracoids. The latter are well ossified, stout, straight shafts, strongly and equally expanded at both ends, as contrasted with the more expanded mesial ends in *Thoraciliacus*. The two coracoids meet mesially. The scapula is small, roughly triangular, uncleft and intensely ossified. It resembles, but is wider than, the scapula of *Thoraciliacus*. The suprascapula is faintly ossified, triangular in shape; it supports a V-shaped cleithrum,

having two well-ossified prongs, the posterior being stouter and shorter than the anterior (Pl. 9 B). No traces of sternum, episternum, or coracoidal cartilages were found.

Pelvic girdle (Fig. 11 B; Pl. 9 E). The pelvis forms a distinct triangle whose head angle is roughly 45°. The pelvic articulation being acroiliac, there is no functional synsacrum. (This is the fundamental difference between *Cordicephalus* and *Thoraciliacus*.) The tips of the ilia articulate with the sacral diapophyses only, having, in most cases, no projection anterior to the latter. In the few cases found of forward projection, the anterior slope of the ilia was apparently either natural, due to forward sliding of the ilia during movement (see p. 276), or an artificial shift caused by fossilization. The pubis is strongly ossified, and the ischium forms a medium-sized rear extension.

Limbs (Fig. 13 B; Pls. 7 A, B, 8 A). *Cordicephalus* does not differ essentially in its limbs from *Thoraciliacus* apart from slight differences in shape of particular bones and its generally more slender build.

Forelimb. The humerus is straight, smooth, and round in cross-section; distally, it has a well-ossified, developed, spherical capitate eminence (Pl. 9 B). The radioulna is single, flat, expanded at both ends, grooved throughout, and has a prominent olecranon. There are nine carpals arranged in three rows (Pl. 9 H). The two proximal rows comprise four big elements: radiale, ulnare, and two centrales. The inner centrale is diagnostically triangular, projecting distinctly to the rear. The five distal carpals involve four bones corresponding to each of the fingers, and one prepollex carpal. Again as in *Thoraciliacus*, the fourth distal carpal is the largest, diagnostically triangular, while the rest are essentially small spheres. There are four subequal fingers involving four very long and slender metacarpals, and 2, 2, 3, 3 phalanges, the terminals being pointed.

Hindlimb. The femur is slightly sigmoid in shape, expanded towards both ends. The tibiofibula is slightly shorter than the femur and is grooved throughout. The tibiale-fibulare are elongated, fused at both ends, leaving a conspicuous interosseous space throughout. The five distal tarsals involve a large centrale, the tarsal of a prehallux, and three smaller bones corresponding to the three inner metatarsals, the second being the largest. There are five toes with remarkably long and slender metatarsals, and 2, 2, 3, 4, 3 phalanges, the terminals being pointed. A rudimentary prehallux consists of only one small metatarsal.

Cordicephalus longicostatus sp. nov.

Figs. 8, 9, 10–13; Pls. 10, 11; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology, No. F 171, crushed skeleton including parts of skull, column, girdles and limbs.

Hypodigm. Type and specimens F 150, 152, 156, 171, 173, 188, 189, 192–196, 251, 252.

Horizon and locality. Same as for *Thoraciliacus rostriceps*.

Specific diagnosis. Very similar to *Cordicephalus gracilis* from which it differs in its larger size and details of skull. See Table 5 for statistically significant differences between the two species. *C. longicostatus* is further diagnosed, as against *C. gracilis*, by having: a slight rostrum; large, subquadrangular nasals; slender frontoparietals; parasphenoid hornless at base of blade; sphenethmoid devoid of prominent anterior projection; otic capsules subquadrangular; long ribs; small cleft scapulae; suprascapulae posteriorly rounded; ilia divergent only to about 30°.

Description of type material. Badly preserved, crushed, small frog, represented by original bones impregnated by brown limonitic ferric oxides.

Skull (Fig. 10 A). The skull is similar to that of *C. gracilis*, from which it differs in the following characters: the subquadrangular nasals form a small triangular ros-

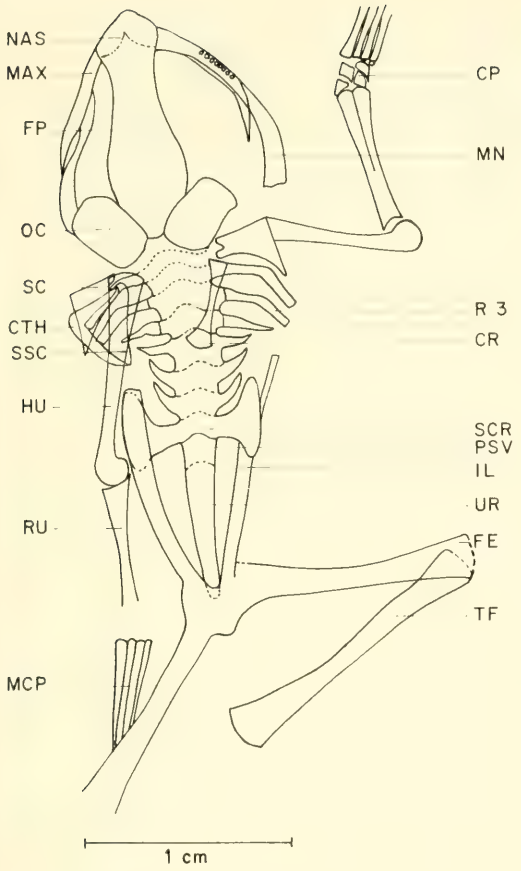


Figure 8. *Cordicephalus longicostatus*, HUJZ, F 171, type specimen. Abbreviations: CP-carpal; CR-coracoid; CTH-cleithrum; FE-femur; FP-frontoparietals; HU-humerus; IL-ilium; MAX-maxilla; MCP-metacarpal; MN-mandible; NAS-nasal; OC-otic capsule; PSV-postsacral vertebra; R3-rib 3; RU-radioulna; SC-scapula; SCR-sacrum; SSC-suprascapula; TF-tibiofibula; UR-urostyle.

trum. The anterior margin of the sphenethmoid is shallow, less prominent, and the frontoparietals are vase-shaped and more slender than in *C. gracilis*. No describable remains were preserved of the pterygoid, quadrate, or vomer. The palatines and quadratojugals are absent. The parasphenoid apparently lacks the processes on base of blade and hilt. The otic capsules are subquadrangular; their axes form an acute angle. In F 188 there is a bent plectrum of columella, 2.3 mm long and 0.3 mm wide, having a swollen base (Pl. 11 B, E).

Vertebral column (Fig. 11 A). There are eight opisthocoelous presacral vertebrae. The atlas has no appendages. The transverse processes of presacrals six through eight resemble, but are slightly larger than, those of *C. gracilis*. The four pairs of ribs are a larger replica of the latter (Pl. 11 A, D). The sacrum consists of the ninth opisthocoelous vertebra, having strongly expanded diapophyses; the latter are connected to the centrum through a narrow bridge of bone broadening abruptly distally (Pl. 11 F). The urostyle is free from the sacrum, articulating with the latter by a single condyle. It may contain one to two postsacrals or lack them entirely.

Pectoral girdle (Fig. 12 A). The girdle is arciferal. The clavicles are strongly arched. The coracoids diverge strongly from the clavicles, being well-ossified, stout, straight shafts expanded at both ends but more so mesially. The scapula is small, roughly triangular, and cleft in all three analyzable specimens (F 171, Pl. 10; F 188, Pl. 11). The suprascapula is faintly ossified, having a rounded posterior margin rather than a triangular one as in *C. gracilis*. The suprascapula supports a well ossified V-shaped cleithrum. No traces of episternum, sternum, or coracoidal cartilages were found.

Pelvic girdle (Fig. 11 A). The pelvic articulation is acroiliac, the tips of the ilia articulating with the sacrum. The pelvis forms an elongated triangle whose head angle is roughly 30°. In both features of the pelvis it is distinguishable from *C. gracilis*, whose pelvis is shorter, having a head angle of roughly 45°. The pubis and ischium are strongly ossified. No traces of epipubis were found.

Limbs (Fig. 13 A). No essential meristic characters distinguish the limbs from those of *C. gracilis*, but differences do occur in shape and size. The humerus is a straight, very long, smooth shaft, expanding only near its ends, being subequal in diameter

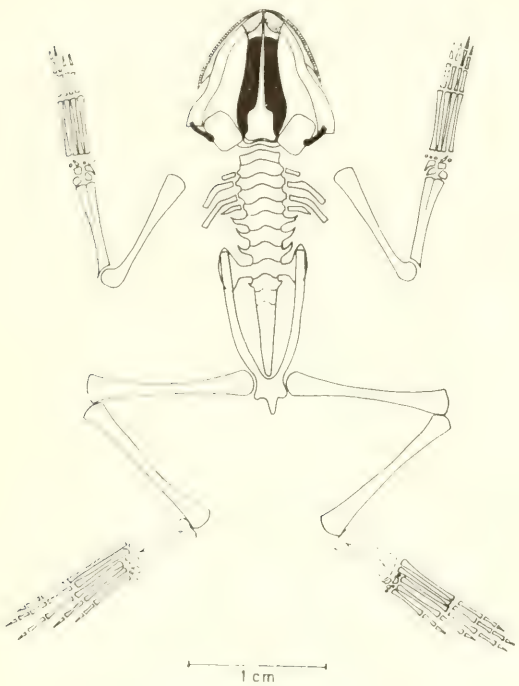


Figure 9. *Cordicephalus longicostatus*, reconstruction.

throughout its length. The capitate eminence is well developed. The radioulna is relatively long, having a well-developed olecranon process (Pl. 11 C). There are nine carpals and four subequal fingers involving very long metacarpals, as in *C. gracilis*. In no specimens were the phalanges entirely preserved; the phalangeal formula is thus indeterminable. The terminal phalanges are pointed. The femur is faintly sigmoid in shape, greatly expanded at both ends, being slightly larger than the tibiofibula; the latter is grooved throughout. The tibiale and fibulare are relatively long. The five metatarsals are very long; the terminal phalanges are pointed.

OSTEOLOGICAL SUMMARY

The following list summarizes for each skeletal system the characters common to all three species, and also the skull, pelvis, and tarsal features distinguishing *Cordicephalus* from *Thoraciliacus*. (Shape differences between the two genera are not repeated. See Tables 6 and 7 for qualitative differences in skull and pelvis, Tables 4 and 5 for quantitative differences between *Cordicephalus* and *Thoraciliacus*.)

SKULL (Fig. 10)

1) Skull well ossified, broader than long.
2) Frontoparietals large, vase-shaped, azygous.
3) Premaxillae and maxillae dentigerous.
4) Maxillary arcade incomplete.
5) Otic capsules extensive.
6) Plectrum of columella well ossified and developed, slightly curved rod.
7) Pterygoids extensive, with a long anterior extension.
8) Parasphenoid sword-like, having only short basal processes.
9) Sphenethmoid single, pointed anteriorly.
10) Vomers paired and edentulous.
11) Quadrate subquadrangular and well ossified.
12) Nasals well developed, medium to broad in shape, forming a *prominent* rostrum only in *Thoraciliacus*.
13) Squamosals reduced.
14) Quadratojugals, palatines and mentomandibulars absent.
15) Mandible edentulous, consisting of a slender dentary and a stronger prearticular.
16) Supra-otic arm, annulus tympanicus and hyobranchial skeleton were not found.

VERTEBRAL COLUMN (Fig. 11)

17) Eight presacral vertebrae.
18) Sacrum consists of the ninth vertebra having greatly expanded diapophyses.
19) Postsacral vertebrae one in *Thoraciliacus*, or two in *Cordicephalus*.
20) Centrum ectochordal.
21) Vertebrae opisthocoelous.
22) Sacro-urostylar articulation free and

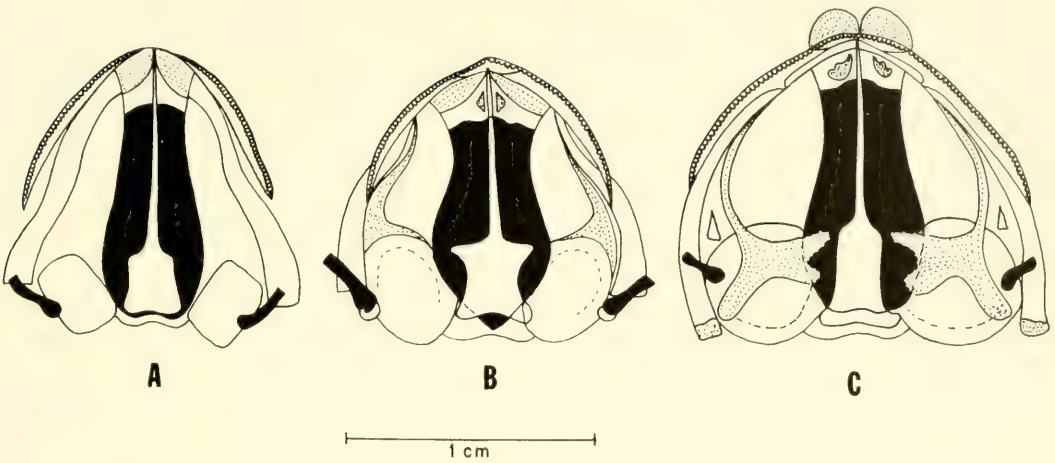


Figure 10. Reconstruction of the skulls of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*. Solid black and stippling are used to distinguish bones and do not imply the nature of substance.

monocondylar.

23) Four pairs of free ribs corresponding to presacrals two through five.
24) Rib fusions with their corresponding transverse processes occasionally occur.
25) Successive vertebrae not fused.

PECTORAL GIRDLE (Fig. 12)

26) Pectoral girdle inferred arciferal.
27) Clavicles and coracoids strongly divergent.
28) Coracoids with strong shafts expanded at both ends.
29) Clavicles large and strongly arched.
30) Clavicles and coracoids meet midventrally.
31) Scapula small and mostly uncleft.
32) Suprascapula a large petaloid blade.
33) Cleithrum large, V-shaped.
34) Sternum, episternum and coracoidal cartilages absent.

PELVIC GIRDLE (Fig. 11)

35) Pubis ossified.
36) Ilia long in *Thoraciliacus*, relatively short in *Cordicephalus*.
37) Pelvic articulation either iliocostal (= medioiliac, in *Thoraciliacus*) or acroiliac (in *Cordicephalus*).
38) Ischium relatively long.
39) Epipubis absent.

FORELIMB (Fig. 13)

40) Humerus straight, mostly smooth, having a well-developed spherical capitate eminence.
41) Radioulna single, flat, expanded at both ends, having a prominent olecranon.
42) Nine free carpals.
43) Four fingers with very long metacarpals, 2, 2, 3, 3 phalanges, the terminals being pointed.
44) Prepollex represented by its carpal only.

HINDLIMB (Fig. 13).

45) Femur faintly S-shaped, having a low, short femoral crest.
46) Tibiofibula single, strong, slightly shorter than the femur.
47) Tibiale and fibulare are elongated, fused at the two ends.
48) Five free distal tarsals.
49) Five toes with very long metatarsals,

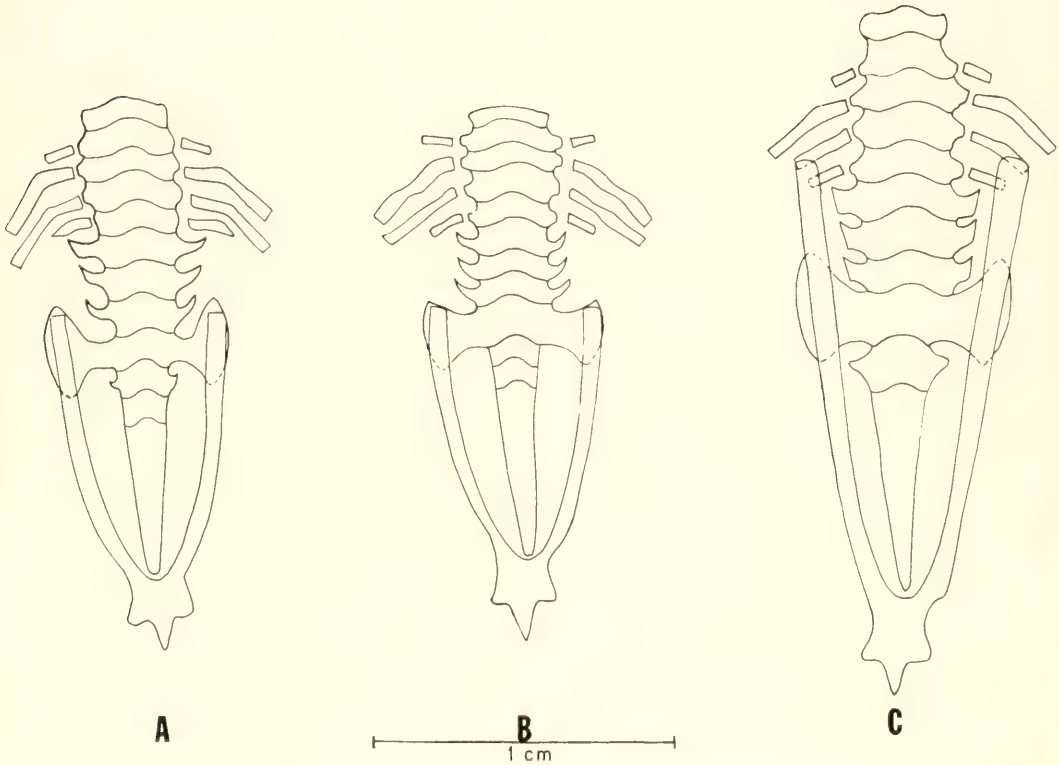


Figure 11. Reconstruction of the vertebral column and pelvis of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*.

2, 2, 3, 4, 3 phalanges, the terminals being pointed.

50) Prehallux represented by a metatarsal in *Cordicephalus*, but only by a tarsal in *Thoraciliacus*.

51) Epiphyses of long bones well ossified.

VARIATION

Both inter- and intra-populational variations are evident in the three sympatric populations of Ramon frogs. The morphological differences described above (diagnoses, Table 6, 7, and Figs. 4–13) provide the qualitative taxonomic differential evidence. Statistically significant differences of several variates (Tables 4, 5; Fig. 16), support the qualitative deductions. The *interpopulational* qualitative and quantitative differences are explicable only on the assumption of three coexisting related taxa, and rule out any sex or age alternative explanations.

The availability of large samples, particularly for *Thoraciliacus*, permitted the study of intrapopulational variation of size, shape, and meristic characters in Ramon frogs. The detailed study will be reported elsewhere. All three Ramon samples are homogeneous as regards place, environment, and time, but heterogeneous with regard to sex, age, and individuals. Meristic variations appear in Figure 14, and size-shape variations of the vertebral column and pelvis in Figure 15.

The univariate statistics of the three populations are shown in Table 3. The coefficients of variation ($V = 100\ s/\bar{x}$) are averaged for all variates and for each skeletal system of the three species in Figure 16.

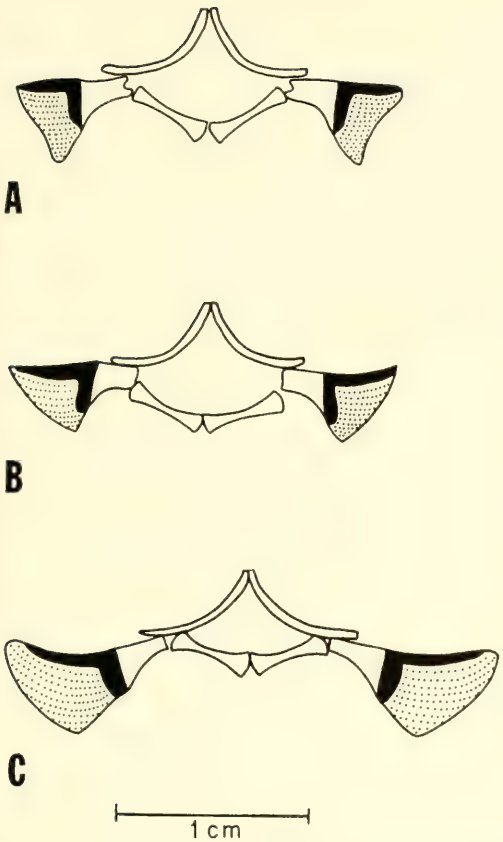


Figure 12. Reconstruction of the pectoral girdles of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*. The cleithrum is indicated in black; the suprascapula is stippled.

Skull. Shape variation is prominent in the frontoparietals, columella, and particularly in the squamosals. Remarkable individual variation is found in the frontoparietals. Four out of 62 specimens, or 6.5 per cent, of *Thoraciliacus* have a median suture in these usually azygous bones (e.g. in F 42, 32, 148 ?, 258). A small median oval foramen in specimens F 14, 54 ?, 56, 341 might represent the parietal foramen, which may not have been preserved in other specimens. Numerous small round holes show in each of the frontoparietals of six specimens (F 42, 45, 98, 133, 134, 213). Their nature is obscure. Teeth vary in number in the maxilla (33–37; mean = 35), and premaxilla (8–10).

Vertebral column (Figs. 11, 14, 15). Size, shape, and meristic variation are evident in each part of the column but are most striking in the urostyle. Eight presacrals characterize all three species, yet one or two specimens (F 112, on Fig. 15, and 127 ?) out of 256, or 0.8 per cent, have nine presacrals. All analyzable centra proved opisthocoelous in 261 skeletons, but many vertebrae are not determinable. The sacral diapophyses in 239 out of 250, or 95.6 per cent, are symmetrically attached to the ninth vertebra. The remaining 11 specimens display individual variation of right-left asymmetry of the diapophyses on the ninth vertebra only, or involving the 8th, and 10th vertebrae, as well (Figs. 14, 15). Successive vertebrae are not fused throughout the column. Ribs display striking individual variations in shape, size, and direction, and presumably age variation in fusions with their diapophyses. The older the animal the more fusions occur, particularly in ribs 1 and 4. The atlas is normally ribless, yet in 17 out of 232 cases, or 7.3 per cent, it has small and simple ribs or just diapophyses (Fig. 15, F 60). The second rib of *Thoraciliacus* is the longest in 138 out of 181 cases. In 43 specimens, or 23.75 per cent, the third is the longest. The urostyle may be wide and short or long and narrow. The proximal portion tends as a rule to have postsacral vertebrae, diapophyses or both. Out of 184 cases, 178, or 96.73 per cent, display postsacrals; the rest are apparently smooth indivisible rods. In *Thoraciliacus*, 140, or 76.08 per cent, have one postsacral, with or without diapophyses. In *Cordicephalus*, 3 out of 9, or 68.4 per cent, have two postsacrals; for other variations and their frequencies, involving up to four postsacrals, refer to Figures 14 and 15, and Plate 6 B.

Pectoral girdle (Fig. 12). The scapula is the most variable component of the pectoral girdle of the three species. Normally its proximal margin is uncleft; yet cleft

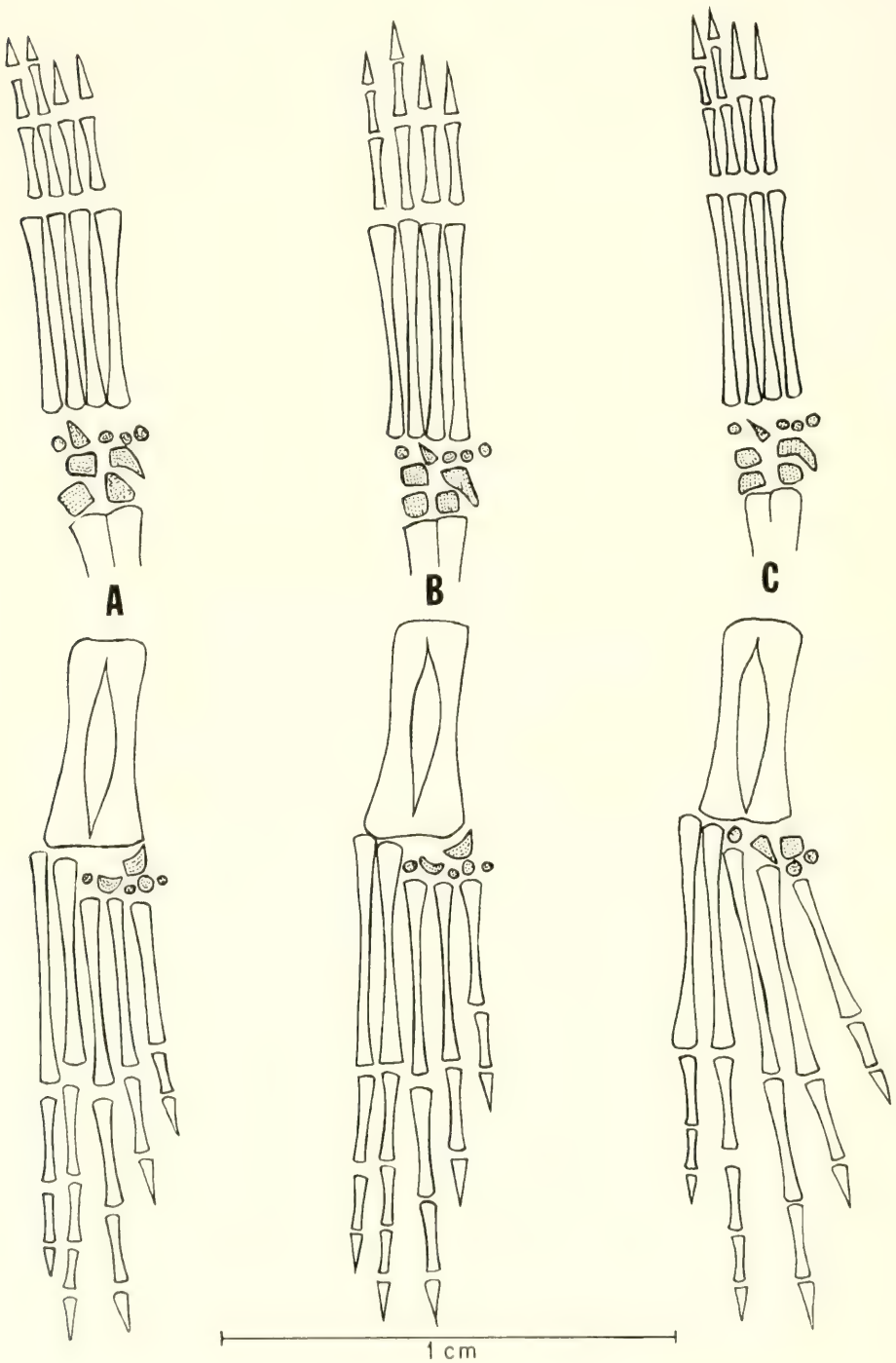


Figure 13. Reconstruction of the manus (upper three drawings), and pes and tarsus (lower three drawings) of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*.

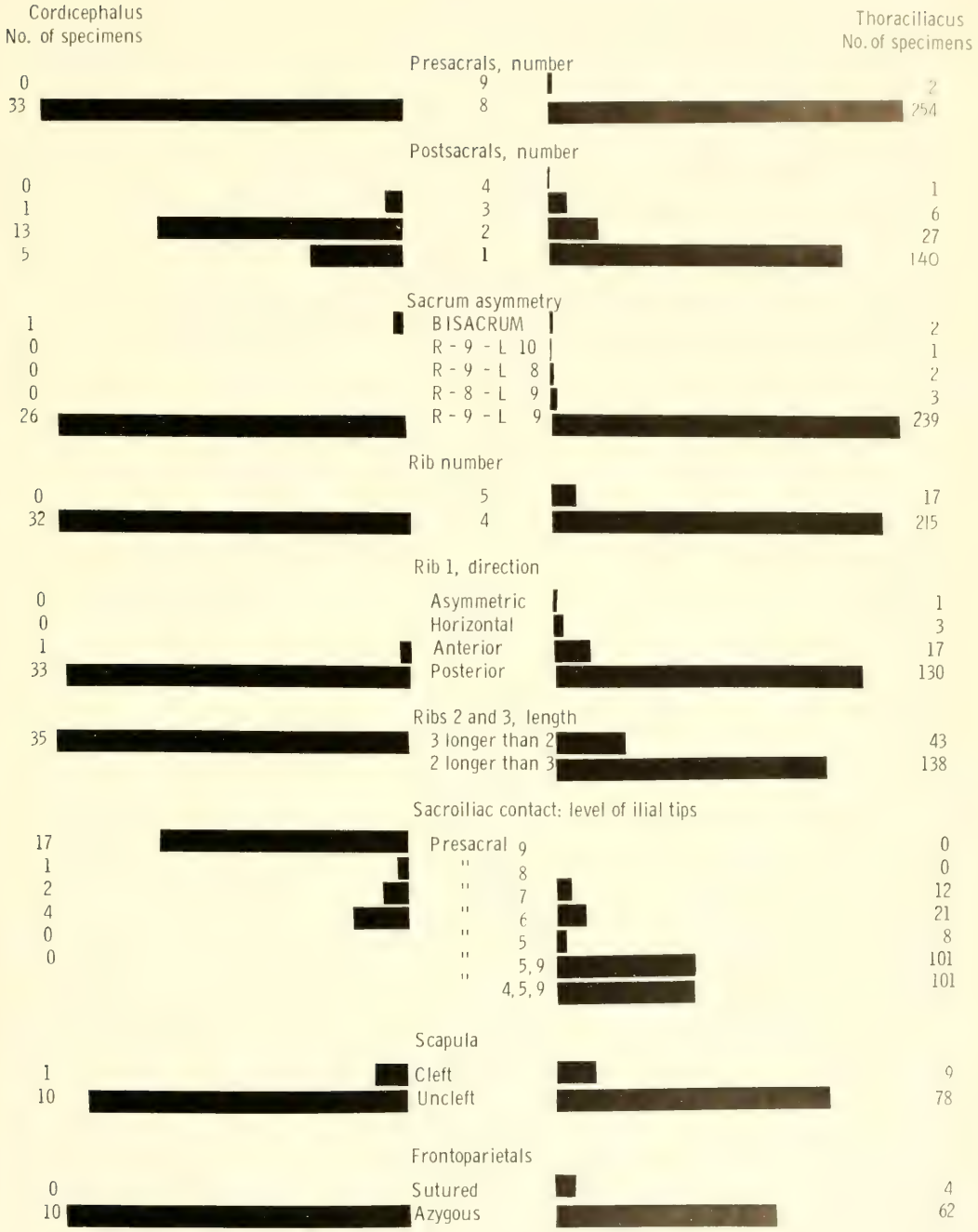


Figure 14. Meristic variations in *Thoraciliacus rostriceps* and *Cordicephalus gracilis*. Horizontal bars indicate percentages; the numbers on the right and left sides are of specimens. Figure 15 shows some of the variants whose frequencies appear above.

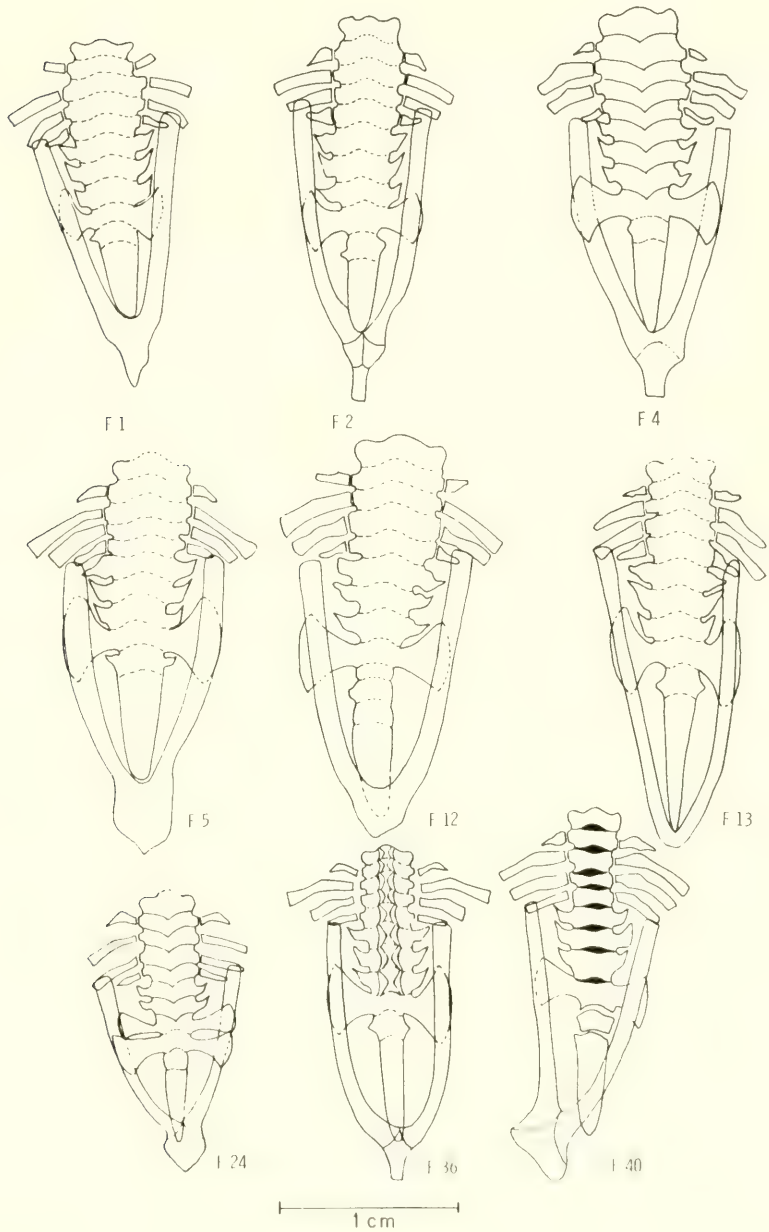
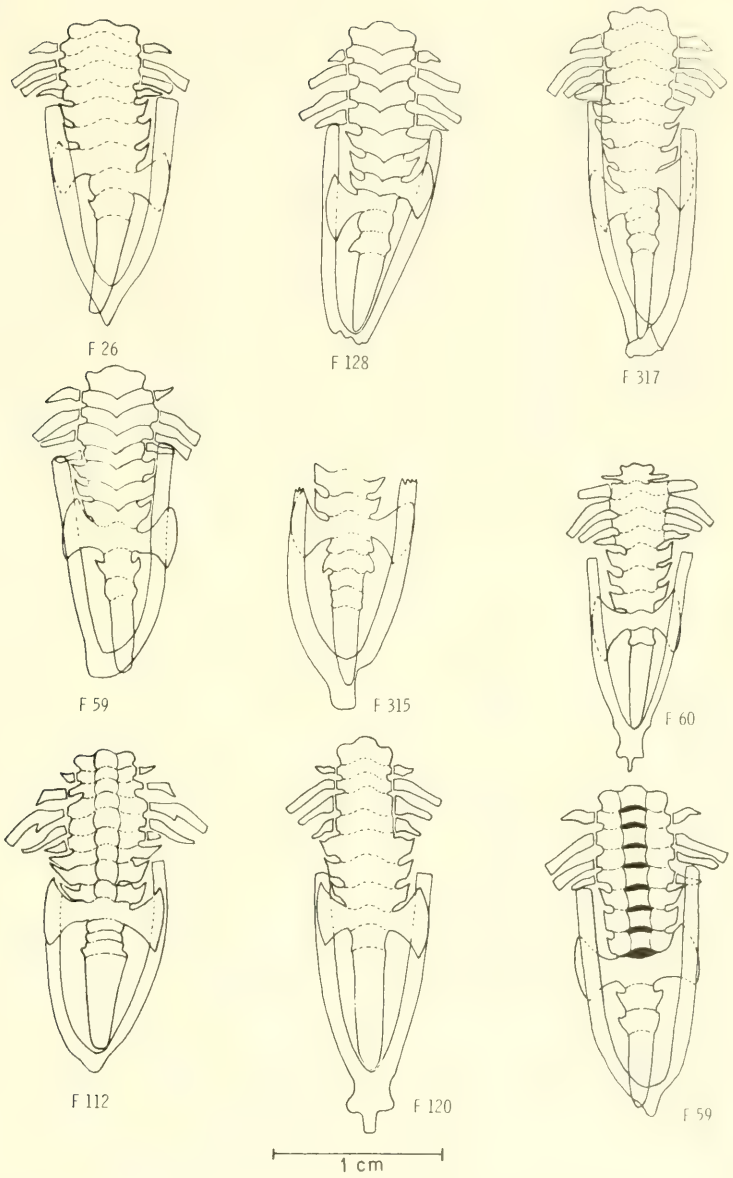


Figure 15. Variations in the vertebral column and pelvis of *Thoraciliacus rostriceps*. For frequencies of the presented cases refer to Figure 14. Note variation in shape of ribs, ilia, sacrum, urostyle. F 1—iliocostal articulation; ilia contact extensions of presacrals 4, 5, 9. F 2—iliocostal articulation as for F 1; note puboischium complex. F 4—dorsal aspect; iliocostal articulation, the ilia contact the extensions of presacrals 5, 9. F 5—rib 2 longer than 3; postsacral with diapophyses. F 12 three postsacrals. F 13 asymmetry of sacral diapophyses on vertebra 9. F 24 bisacrum. F 36—ecto



chordal centra. F 40—black indicates matrix; note asymmetry of sacral diapophyses. F 26—sacral asymmetry: right sacral diapophysis on vertebra 9; left sacral diapophysis on vertebra 8; abbreviated on Figure 14 to: R-9–L-8. F 128—sacral asymmetry: R-8–L-9. F 317—sacral asymmetry: R-9–L-10. F 59—two postsacrals; asymmetry of rib one. F 315—four postsacrals. F 60—five ribs (additional rib on the atlas). F 112—five ribs; nine presacrals; three postsacrals. F 120—tips of ilia reach level of presacral seven. F 59—counterpart; black indicates matrix; two postsacrals with diapophyses.

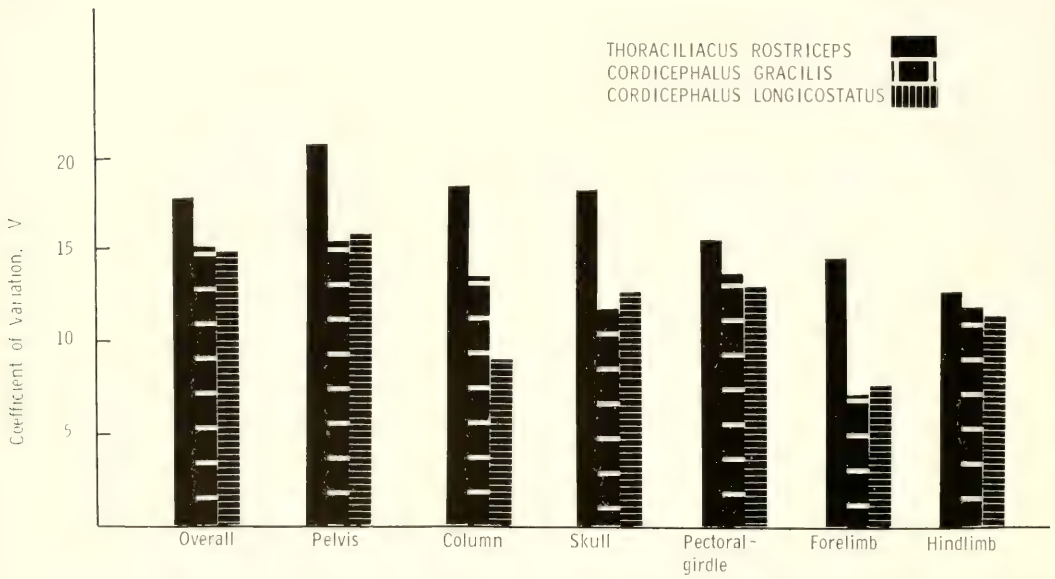


Figure 16. Mean V, coefficient of variation, of the three Ramon species, for the whole skeleton, and for each skeletal system.

scapulae show in 9 out of 78 cases, or 11.5 per cent, of *Thoraciliacus*; in 1 out of 11 in *Cordicephalus gracilis*, and in all of the three analyzable cases of *C. longicostatus* (Pl. 11 E).

Pelvic girdle (Figs. 11, 14, 15). The pelvic articulation is highly variable in *Thoraciliacus*. The tips of the ilia make contact with ribs 3 and 4 (Pl. 6 A) in 101 out of 243 cases, or 41.6 per cent, and with only the 4th rib (Pl. 6 E) in another 41.6 per cent, amounting to 83 per cent iliocostal contact in all. In the remaining 17 per cent the ilia end freely at the level of presacrals 5, 6, and 7 (Pl. 4). The great variation is reflected in the high V of presacral ilium of 26.93 (Table 3).

Limbs. The limbs display the least meristic and continuous variation in the whole skeleton (Figs. 13, 16).

In summary, *Thoraciliacus* is more variable than *Cordicephalus* in both meristic and continuous variations (Figs. 14, 16). The coefficient of variation (V) is 18.05 in *Thoraciliacus rostriceps* (average of 28 variates), versus 15.90 in *Cordicephalus gracilis*, and 15.75 in *C. longicostatus* (average of 25 and 24 variates respectively). The different skeletal systems within a species display differential amounts of variation. In all three species the pelvis is the most, the limbs are the least, variable. Other skeletal systems differ in order of decreasing amount of variations among the three species (Figure 16).

DISCUSSION

Relationships and Evolutionary Interpretation of Ramon Frogs

General. The characters listed in the osteological summary indicate that the three Ramon species are closely related and may be referred to the same family. Each skeletal system will now be evaluated for taxonomic relationships, variation, adaptation, and phylogeny, in order to assess the evolutionary significance of Ramon frogs. The evaluation of the taxonomic criteria and their significance is largely based on the critical review of Griffiths (1963).

The precise Paleozoic ancestry of Anura is uncertain (Parsons and Williams, 1963),

TABLE 2. MEASUREMENTS IN MILLIMETERS OF THE TYPE SPECIMENS

Variate	*Thoraciliacus rostriceps* HUJZ No. F 93	*Cordicephalus gracilis* HUJZ No. F 165	*Cordicephalus longicostatus* HUJZ No. F 171
Head + body length	41.4	30.3	31.0
Skull length	14.5	10.6	11.8
Skull width	14.5	12.0	11.5
Otic capsule length	5.0	5.1	5.0
Otic capsule width	4.2	3.4	3.0
Vertebral column length	11.6	9.0	10.5
Urostyle length	11.0	7.8	9.4
Humerus length	11.0	9.2	10.0
Radioulna length	8.4	6.2	7.3
Metacarpalia length	6.2	5.0	5.8
Clavicle length	6.2	–	–
Coracoid length	4.6	–	4.9
Scapula length	3.6	3.0	2.9
Scapula width	2.4	2.2	2.5
Femur length	13+	12.8	13.0
Tibiofibula length	–	12.2	13.0
Tibiale-fibulare length	–	5.0	5.6
Metatarsalia length	–	6.6	6.0
Sacral diapophysis length	4.1	4.1	4.0
Sacral diapophysis width	3.0	2.9	2.4
Puboischium length	4.4	2.8	3.6
Presacral ilium length	3.6	0.7	–
Ilium length	17.4	11.0	12.2

SPECIFICATION OF MEASUREMENTS.

Head + body length. The distance from tip of snout to tip of ischium.

Skull length. The distance from tip of snout to posterior margin of exoccipital condyles.

Skull width. The maximum distance between the outer margin of the prearticular along a line normal to mid-otic capsules.

Vertebral column length. The distance from tip of atlas to tip of sacrum.

Clavicle length. The least distance between tips of clavicles.

Scapula length. The total distance of the diagonal outer margin of scapula.

Scapula width. The minimum distance between the anterodistal point of scapula to the proximal uncleft margin.

Sacral diapophysis width. The distance from the lateral margin of the centrum to the distal margin of the diapophysis along a line normal to the centrum.

Puboischium length. The distance from tip of pubis to tip of ischium.

TABLE 2. *Continued*

Ilium presacral length. The length from the anterior tip of the sacral diapophysis to the anterior tip of the ilium.

All other dimensions are the maximum distances between parallel planes tangential to the designated anatomical elements: urostyle, humerus, radioulna, metacarpal, metatarsal, tibiofibula, tibiale-fibulare, etc.

yet amphibamids (Griffiths, 1963, and his references; Estes, 1965) or branchiosaurids (Noble, 1931; Reig, 1964) are possible ancestors. On the other hand, the early Triassic *Triadobatrachus* (= *Protobatrachus*, name preoccupied, Kuhn 1962) seems to be a plausible proanuran ancestor (Griffiths, 1963; Tihen, 1965), despite some recent doubts (Hecht, 1962). The earliest known true frog, *Vieraella herbstii* Reig, from the early Jurassic of Argentina indicates that the anuran grade evolved in pre-Jurassic times. The still undocumented transition from proanurans to anurans took place presumably during the Triassic. In the following discussion I will refer to labyrinthodonts, *Triadobatrachus*, and Jurassic frogs as the points of reference by which to distinguish primitive from specialized characters. All references to *Triadobatrachus* and *Notobatrachus* are to Piveteau (1937) and Reig (1957), respectively, unless otherwise specified.

Skull. The skulls of the three Ramon species have many more features in common than those separating them. This is evident from the similarities given in the osteological summary and the differences as shown in Table 6. The differences are either specific or, at most, generic in rank.

In most characters the skulls of all three species agree with the skulls of Recent pipids (Paterson, 1939, 1945, 1955, 1960). The character complex indicative of pipid affinities comprises: *azygous frontoparietals; developed columella; large otic capsules; an incomplete maxillary arcade; reduced maxillae, vomers, and squamosals;*

TABLE 3. MEASUREMENTS OF *THORACILIACUS ROSTRICEPS*, *CORDICEPHALUS GRACILIS*, AND *CORDICEPHALUS LONGICOSTATUS*, IN MILLIMETERS

Variate	N	Range	Mean ($\bar{x}$)	Standard Error ($S_{\bar{x}}$)	Standard Deviation (s)	Coefficient of Variation (V)
		A. *Thoraciliacus rostriceps*				
Head + body length	118	20.5–51.5	32.49	0.49	5.38	16.56
Skull length	126	6.6–17.0	12.05	0.17	1.95	16.24
Skull width	122	9.2–18.2	12.79	0.15	1.76	13.76
Otic capsule length	140	2.4– 6.9	4.32	0.06	0.81	18.92
Otic capsule width	141	2.6– 6.8	4.21	0.06	0.80	18.98
Orbit length	88	2.8– 8.4	5.53	0.13	1.06	19.21
Orbit width	88	1.4– 5.2	3.01	0.08	0.75	25.05
Interorbital space	64	2.5– 6.5	4.05	0.12	0.97	23.94
Vertebral column length	170	7.0–17.8	11.01	0.13	1.78	16.17
Urostyle length	121	5.0–12.4	8.03	0.15	1.70	21.19
Urostyle width	105	1.0– 3.3	2.02	0.04	0.45	22.60
Puboischium length	82	1.2– 5.6	2.90	0.08	0.78	27.18
Humerus length	158	6.4–13.0	9.65	0.11	1.41	14.65
Radioulna length	138	4.4– 9.3	6.76	0.08	1.02	15.10
Metacarpalia length	84	4.0– 7.9	5.72	0.09	0.88	15.46
Clavicle length	42	3.3– 6.6	4.79	0.12	0.78	16.30
Coracoid length	74	3.0– 6.3	4.39	0.07	0.63	14.35
Scapula length	105	1.7– 4.2	3.04	0.05	0.50	16.59
Scapula width	100	1.5– 3.5	2.45	0.04	0.43	17.86
Femur length	114	10.0–19.0	13.47	0.14	1.60	11.88
Tibiofibula length	88	9.5–16.7	13.00	0.17	1.61	12.44
Tibiale-fibulare length	69	4.0– 8.8	6.18	0.11	0.96	15.56
Metatarsalia length	52	4.3– 8.3	6.40	0.11	0.85	13.28
Sacral diapophysis length	138	2.4– 6.7	3.92	0.06	0.78	19.92
Sacral diapophysis width	142	1.2– 4.4	2.55	0.04	0.50	19.64
Ilium length	138	9.0–19.6	13.72	0.17	2.08	15.25
Ilium presacral length	147	1.0– 6.7	3.25	0.07	0.87	26.93
Ilium width	125	0.7– 1.7	1.07	0.01	0.22	20.59
		B. *Cordicephalus gracilis*				
Head + body length	30	22.5–31.5	26.05	0.42	2.32	8.92
Skull length	21	8.4–11.7	9.87	0.22	1.03	10.53
Skull width	17	8.7–13.0	10.63	0.32	1.35	12.76
Otic capsule length	32	3.3– 5.1	4.14	0.08	0.50	12.10
Otic capsule width	34	3.0– 4.4	3.76	0.07	0.41	11.06
Orbit length	12	3.6– 6.0	4.70	0.20	0.69	14.68
Orbit width	12	2.1– 3.5	2.71	0.12	0.44	16.37
Vertebral column length	41	7.4– 9.8	8.69	0.08	0.50	5.76
Urostyle length	24	4.7– 8.8	6.70	0.23	1.17	17.49
Urostyle width	28	1.0– 2.4	1.51	0.05	0.29	19.35
Puboischium length	13	1.3– 2.8	2.10	0.12	0.50	21.38
Humerus length	26	7.5–10.0	8.70	0.11	0.60	6.94
Radioulna length	23	5.2– 7.0	6.20	0.11	0.56	9.05
Metacarpalia length	17	3.8– 6.2	4.98	0.15	0.65	13.09
Clavicle length	2	3.6– 4.5	4.05	0.45	0.63	15.71
Coracoid length	14	3.1– 5.2	4.07	0.16	0.59	14.65
Scapula length	15	2.0– 3.0	2.48	0.09	0.35	14.15
Scapula width	16	1.7– 2.7	1.90	0.06	0.25	13.45
Femur length	20	10.0–13.8	11.40	0.26	1.18	10.39
Tibiofibula length	17	9.8–13.2	11.10	0.23	0.96	8.69
Tibiale-fibulare length	16	4.3– 6.2	5.15	0.13	0.55	10.69
Metatarsalia length	14	4.5– 6.7	5.89	0.17	0.63	10.82

TABLE 3. *Continued*

Variate	N	Range	Mean ($\bar{x}$)	Standard Error ($S_{\bar{x}}$)	Standard Deviation (s)	Coefficient of Variation (V)
Sacral diapophysis length	33	2.7– 4.6	3.45	0.08	0.49	14.21
Sacral diapophysis width	36	2.1– 3.3	2.65	0.05	0.31	11.89
Ilium length	26	8.2–11.8	10.21	0.19	0.97	9.57
Ilium presacral length	22	0.0– 1.7	0.42	0.11	0.52	–
Ilium width	26	0.7– 1.2	0.92	0.02	0.12	13.84
	C. *Cordicephalus longicostatus*					
Head + body length	9	28.0–33.0	31.44	0.55	1.66	5.30
Skull length	6	9.0–11.9	10.40	0.48	1.20	11.52
Skull width	4	11.5–12.5	12.00	0.20	0.40	3.40
Otic capsule length	10	3.5– 5.0	4.31	0.15	0.48	11.23
Otic capsule width	9	3.0– 5.0	3.85	0.25	0.76	19.93
Orbit length	3	5.6– 7.0	6.36	0.40	0.71	11.14
Orbit width	2	4.0– 4.6	4.30	0.30	0.42	9.87
Vertebral column length	14	9.0–12.0	10.15	0.20	0.78	7.74
Urostyle length	8	8.0– 9.9	8.95	0.21	0.60	6.78
Urostyle width	10	1.5– 2.3	1.71	0.07	0.23	13.91
Puboischium length	6	2.5– 4.3	3.28	0.25	0.61	18.82
Humerus length	12	8.5–12.0	10.19	0.28	0.98	9.65
Radioulna length	10	6.1– 8.5	7.44	0.22	0.71	9.68
Metacarpalia length	8	5.3– 6.0	5.61	0.10	0.29	5.25
Clavicle length	1	5.3	5.30	–	–	–
Coracoid length	7	3.5– 4.9	4.21	0.19	0.50	12.05
Scapula length	5	2.3– 3.0	2.70	0.14	0.32	12.00
Scapula width	4	2.1– 2.5	2.27	0.08	0.17	7.51
Femur length	6	11.0–13.0	12.23	0.29	0.70	5.80
Tibiofibula length	4	10.1–13.0	11.90	0.69	1.39	11.70
Tibiale-fibulare length	3	5.3– 5.8	5.56	0.14	0.25	4.52
Metatarsalia length	2	5.5– 6.0	5.75	0.25	0.35	6.15
Sacral diapophysis length	9	3.2– 4.3	3.72	0.11	0.35	9.38
Sacral diapophysis width	10	2.4– 3.8	3.07	0.12	0.40	13.03
Ilium length	11	9.7–12.6	11.71	0.25	0.84	7.19
Ilium presacral length	8	0.0– 2.5	0.48	0.33	0.94	–
Ilium width	10	1.0– 1.4	1.13	0.05	0.16	14.48

absence of palatines, quadratojugals, and mentomandibulars; and ossified quadrates. Each isolated character may appear, and vary distinctly, in other families; only the assemblage implies pipid allocation.

Azygous frontoparietals, though universal in pipids, were described also for *Hemisus, Pelobates, Rhinophrynus,* and *Palaeobatrachus.* It is noteworthy that these are either fossorial or aquatic forms. The presence of a suture in the frontoparietals of the Cretaceous *Eoxenopoides, Saltenia,* and possibly *Shelania* was incorporated in the diagnosis of the new pipoid family Eoxenopoididae (Casamiquela, 1961a). Yet paired frontoparietals are displayed by premetamorphic *Xenopus* (Sedra and Michael, 1958), and a median suture is a variable character in *Thoraciliacus* (Fig. 14). Hence both embryology and variation speak against high taxonomic significance for the divided condition, and the character is better included within pipid developmental patterns and variational range.

Ear. Most anurans have complete middle ear bones. Occasionally, however, the columella is missing and only the operculum remains. The latter condition is a feature of the following random assemblage of anurans: *Phryniscus, Hemisus, Cacosternum, Brachycephalus, Pelobates, Rhinophrynus, Bombina,* and ascaphids.

Table 4. Student's *t*-tests Between the Sample Means of the Two Genera *Thoraciliacus* and *Cordicephalus*

Variate	*Thoraciliacus* N	Mean	Standard Deviation	*Cordicephalus* N	Mean	Standard Deviation	Student's *t*	Degrees of Freedom	*P*
Head + body length	118	32.49	5.38	39	27.29	3.16	5.705	155	<.001
Skull length	126	12.05	1.95	27	9.99	1.07	5.293	151	<.001
Skull width	122	12.79	1.76	21	10.89	1.34	4.713	141	<.001
Orbit length	88	5.53	1.06	15	5.03	0.96	1.697	101	.1
Orbit width	88	3.01	0.75	14	2.94	0.71	0.313	100	.7–.8
Otic capsule length	140	4.32	0.81	42	4.18	0.49	1.058	180	.2–.3
Otic capsule width	141	4.21	0.80	43	3.78	0.50	3.349	182	<.001
Vertebral column length	170	11.01	1.78	55	9.06	0.86	7.823	223	<.001
Urostyle length	121	8.03	1.70	32	7.26	1.44	2.328	151	.02
Urostyle width	105	2.02	0.45	38	1.56	0.29	5.775	141	<.001
Puboischium length	82	2.90	0.78	19	2.47	0.74	2.155	99	.02–.05
Humerus length	158	9.65	1.41	38	9.17	1.01	1.978	194	.05
Radioulna length	138	6.76	1.02	33	6.57	0.83	0.977	169	.3–.4
Metacarpalia length	84	5.72	0.88	25	5.18	0.63	2.829	107	.01–.001
Clavicle length	42	4.79	0.78	3	4.46	0.85	0.701	43	.4–.5
Coracoid length	74	4.39	0.63	21	4.12	0.56	1.794	93	.05–.1
Scapula length	105	3.04	0.50	20	2.53	0.34	4.300	123	<.001
Scapula width	100	2.45	0.43	20	1.97	0.28	4.712	118	<.001
Femur length	114	13.47	1.60	26	11.59	1.13	5.658	138	<.001
Tibiofibula length	88	13.00	1.61	21	11.25	1.06	4.711	107	<.001
Tibiale-fibulare length	69	6.18	0.96	19	5.22	0.53	4.177	86	<.001
Metatarsalia length	52	6.40	0.85	16	5.87	0.60	2.310	66	.02
Sacral diapophysis length	138	3.92	0.78	42	3.51	0.47	3.197	178	>.001
Sacral diapophysis width	142	2.55	0.50	46	2.74	0.37	2.409	186	.01–.02
Ilium length	138	13.72	2.08	37	10.65	1.16	8.577	173	<.001
Ilium presacral length	147	3.25	0.87	30	0.43	0.64	16.679	175	<.001
Ilium width	125	1.07	0.22	36	0.98	0.16	2.385	159	.01–.02

The correlation between the absence of the columella and fossorial habits (Eiselt, 1941), either in terrestrial or marginal aquatic habitats, may prove significant, but it needs further evidence. Conversely, pipids have a remarkably developed columella, suggesting its efficacy in purely aquatic habitats.

Most Jurassic and Cretaceous frogs have a columella, indicating its primitiveness in Anura. The *Notobatrachus* case is as yet unsettled (see Casamiquela, 1961a, b, and Hecht, 1963, for negative and positive statements, respectively). Ramon frogs have a large columella linked, at least in *Cordicephalus*, with an operculum, as in Recent *Xenopus*. Presence of middle ear bones appears to be primary, hence primitive.

Extensive otic capsules, varying only in degree, are a feature of all pipoids. Large capsules as an exclusive eoxenopoidid character (Casamiquela, 1961a) are thus ruled out. Hecht (1963: 22) claims that enlarged otic capsules are a feature of "advanced tadpoles and metamorphosing individuals," but large otic capsules characterize all Ramon pipids and the capsule size is positively correlated with total length. The correlation coefficient in *Thoraciliacus* ($N = 80$) is 0.37 ($P < .001$). Hence the extensive otic capsules of pipoids increase in size with age and are not just an embryonic feature but rather a lifelong adaptation especially prominent in adults. Paterson (1960) suggested that the presence of a large otolith in the inner ear sacculus of pipids implied gravitational and

TABLE 5. STUDENT'S *t*-TESTS BETWEEN THE SAMPLE MEANS OF THE TWO SPECIES OF *CORDICEPHALUS*

	Cordicephalus gracilis			*Cordicephalus longicostatus*					
Variate	*N*	Mean	Standard Deviation	*N*	Mean	Standard Deviation	Student's *t*	Degrees of Freedom	*P*
Head + body length	30	26.05	2.32	9	31.44	1.66	6.449	37	<.001
Skull length	21	9.87	1.03	6	10.39	1.19	1.054	25	.3
Skull width	17	10.63	1.35	4	11.99	0.40	1.956	19	.05–.1
Orbit length	12	4.69	0.69	3	6.36	0.70	3.725	13	.01–.001
Orbit width	12	2.71	0.44	2	4.29	0.42	4.678	12	<.001
Otic capsule length	32	4.14	0.50	10	4.30	0.48	0.922	40	.3–.4
Otic capsule width	34	3.76	0.41	9	3.85	0.76	0.464	41	.6–.7
Vertebral column length	41	8.69	0.50	14	10.14	0.78	8.085	53	<.001
Urostyle length	24	6.70	1.17	8	8.94	0.60	5.140	30	<.001
Urostyle width	28	1.51	0.29	10	1.70	0.23	1.934	36	.05–.1
Puboischium length	13	2.09	0.44	6	3.28	0.61	4.752	17	<.001
Humerus length	26	8.70	0.60	12	10.19	0.98	5.738	36	<.001
Radioulna length	23	6.20	0.56	10	7.43	0.71	5.334	31	<.001
Metacarpalia length	17	4.98	0.65	8	5.61	0.29	2.562	23	.01–.02
Clavicle length	2	4.04	0.63	1	5.29	0.00	1.604	1	.3–.4
Coracoid length	14	4.07	0.59	7	4.21	0.50	0.514	19	.6–.7
Scapula length	15	2.47	0.35	5	2.69	0.32	1.234	18	.2–.3
Scapula width	16	1.89	0.25	4	2.27	0.17	2.755	18	.01–.02
Femur length	20	11.40	1.18	6	12.23	0.70	1.613	24	.1–.2
Tibiofibula length	17	11.09	0.96	4	11.89	1.39	1.379	19	.1–.2
Tibiale-fibulare length	16	5.15	0.55	3	5.56	0.25	1.242	17	.2–.3
Metatarsalia length	14	5.89	0.63	2	5.75	0.35	0.304	14	.7–.8
Sacral diapophysis length	33	3.45	0.49	9	3.72	0.40	1.509	40	.1–.2
Sacral diapophysis width	36	2.65	0.31	10	3.06	0.40	3.464	44	.001–.01
Ilium length	26	10.21	0.97	11	11.71	0.84	4.454	35	<.001
Ilium width	26	0.92	0.12	10	1.12	0.16	3.941	34	<.001
Ilium presacral length	22	0.41	0.52	8	0.48	0.94	0.255	28	.8

vibrational responses of the saccular macula. Van Bergeijk (1959) has experimentally demonstrated vibrational responses in the saccular macula due to otolith motions in *Xenopus* tadpoles. Finally, Witschi *et al.* (1953) suggested that the *Xenopus* ear is adapted to underwater sound by its thick adipose tympanal mesenchyme, as well as fit to perceive aerial sound waves that skim along the water surface. It seems possible that the greatly inflated otic capsules of pipoids house air-filled spaces similar to those found in clupeid and mormyrid fishes (Van Bergeijk, 1967) and function as resonators which amplify weak vibrations. Such amplificatory devices of acoustic and vibratory stimuli would be advantageous in water in which amplifying mechanisms of weak air-borne stimuli would be at a premium. It appears that the pipid ear is a specialized aquatic adaptation.

Reduction of some skull bones, such as squamosals and prevomers, is usually associated with great shape variation and is confirmed in Ramon frogs. Such variation may be linked with degenerating characters which have lost all function (Simpson, 1953). Absence of quadratojugals (resulting in an incomplete maxillary arcade) and palatines occurs in various unrelated anurans (Ramaswami, 1939). The absence of these bones seems to imply convergent paedomorphy (Griffiths, 1963) rather than phylogenetic relationship. Certainly all cases of reduced and absent bones are specialized, whether acquired by paedomorphy or by any other genetic mechanism.

A rostrum of variable size occurs in unrelated anurans, e.g., *Bufo typhonius*, *Bufo*

Table 6. Skull Differences of the Three Ramon Species

Species	Skull Outline[1]	Quadrate Region	Nasals	Otic Capsules
Thoraciliacus rostriceps	Spatulate-ovoid	Posterior	Kidney-shaped forming a prominent rostrum	Spherical
Cordicephalus gracilis	Heart-shaped	Anterior	Medium, crescentic no rostrum	Elliptical
Cordicephalus longicostatus	Heart-shaped	Anterior	Broad-ovoid small rostrum	Rectangular

[1] Slight shape differences characteristic of each species occur in the parasphenoid, sphenethmoid, frontoparietals, pterygoids.

granulosus, Triprion petasatus, Pipa pipa, and others. In several tropical species of *Leptodactylus* the rostrum is a sexual character, males using pointed snouts to dig nesting holes for the females. Also, various burrowing frogs have sharp narrow snouts evolved in parallel and convergent lines (Noble, 1931). Burrowing down to two feet depth was reported for *Hemipipa* (Johnson, 1952), suggesting the digging habits in some pipids. Thus the prominent rostrum of *Thoraciliacus* may have been utilized for burrowing in mud bottoms. The flat skull of Ramon frogs may also reflect an aquatic adaptation.

Pipoids share essentially the same skull architecture in spite of shape variation within and between taxa (Table 9). The shape of certain bones may partly indicate intergeneric affinities. The sword-like parasphenoid of Ramon frogs affiliates them with *Xenopus* but segregates them from the broad parasphenoid of *Pipa, Hymenochirus, Shelania,* and the dagger-shaped parasphenoid of *Eoxenopoides* and *Paleobatrachus.* On the other hand, broad nasals are shared by *Thoraciliacus,* "eoxenpoidids," paleobatrachids, *Hymenochirus* and *Pipa,* whereas *Cordicephalus* has medium-size nasals, approximating the narrow *Xenopus* nasals. *Cordicephalus* further shares with *Xenopus* the anteriorly placed quadrate region, and it seems probable that the former type of skull is morphologically ancestral to the latter. On the other hand, the prominent *Thoraciliacus* rostrum coupled with its pelvic specializations make this genus an unlikely ancestor of any Recent pipid.

The skull of Ramon pipids is highly specialized (Table 10) but does not basically differ from the highly specialized skulls of Recent pipids (Paterson, 1955). Judging from gross skull morphology it appears that pipid skulls have evolved little since early Cretaceous times, and their main evolution was presumably Triassic in age.

In summary, the pipid skull is definable by a character-complex. It is specialized to aquatic life by its flatness and large otic capsules and may be paedomorphic. The variations displayed by fossil and Recent pipoids are at most generic in rank and all may be referred to the Pipidae.

Vertebral column. The vertebral column of the three species is basically similar, consisting of eight opisthocoelous presacrals with four pairs of long free ribs (details in the osteological summary; refer to Table 9 for comparison with other pipoids). The three species differ in shape of ribs and diapophyses and in the number of postsacrals (Fig. 11). *Thoraciliacus* has stout ribs and triangular diapophyses in presacrals six through eight and one postsacral, whereas *Cordicephalus* has longer ribs, arcuate diapophyses and, as a rule, two postsacrals. As a whole, the column agrees with the vertebral column of Recent pipids (Noble, 1931; Smit, 1953, and works there cited). However, Ramon frogs are distinguished from all fossil and Recent pipoids by the following character-complex: *ectochordal vertebrae, one or two*

postsacrals, monocondylar sacro-urostylar articulation, and four pairs of free ribs. Each of these characters alone or several combined may occur in other frogs, but the assemblage is unique to *Cordicephalus* and *Thoraciliacus*. The following discussion deals with several aspects of the column.

Presacrals. Non-ascaphoids normally have eight presacrals, with a few generic variants (for pipoids refer to Table 9; for other Anura see Noble, 1931). Thus the presence of eight presacrals in Ramon frogs excludes affinities with ascaphoids, which normally have nine presacrals in the Recent Ascaphidae (Ritland, 1955) as well as in the Jurassic Notobatrachidae (Reig, 1957). Neither the 0.8 per cent of *Thoraciliacus* specimens having nine presacrals (Figs. 14, 15) nor the less than 3 per cent of *Ascaphus* skeletons reported by Ritland to have eight presacrals violate this rule; they rather confirm it by being only individual variants. No correlation is obvious between the number of presacrals in *Anura* and the type of locomotion. Both terrestrial *Oreophrynella* and aquatic *Hymenochirus* have a synsacrum, hence six free presacrals (Noble, 1931). Phylogenetically, however, the number of presacrals, whether eight or nine, reflects an ancient conservative figure, associated presumably with the emerging anuran grade and developed presumably from the 16 or so presacrals of triadobatrachids. All Jurassic and Cretaceous frogs have one or the other of these numbers indicating their primitiveness in Anura.

Opisthocoely is invariable in all 261 studied columns of Ramon frogs. This confirms the constancy of opisthocoely displayed by Recent pipid frogs as opposed to frequent variations in other vertebral patterns (Griffiths, 1963). The articulation patterns of presacrals have been correlated with the mechanics of motion (Gadow, 1933). Thus it appears that terrestrial life involving leaping, walking and climbing forms puts a premium on procoely, whereas opisthocoely and amphicoely are mainly restricted to aquatic and some fossorial forms. However, this correlation is subject to exceptions in both directions and is not yet experimentally supported (Schaeffer, 1949). Phylogenetically, *Triadobatrachus* as well as the known Jurassic frogs are either amphicoelous or opithocoelous, an indication of the primitiveness of these patterns, which appear to have preceded procoely. Hecht's (1963) claim that Jurassic *Notobatrachus* is procoelous, in contrast to its reported amphicoely (Reig, 1957), is disproved by the newly collected amphicoelous notobatrachid material (Casamiquela, 1961b, and personal communication).

Anurans fall into three developmental groups in respect to their vertebral centra, which may be ectochordal, stegochordal, or holochordal (Griffiths, 1963). Ectochordy is a feature of *Triadobatrachus*, ascaphids and rhinophrynids; stegochordy of discoglossids and pipids; and holochordy of all other anurans. The central type is correlatable with the mode of locomotion. Ectochordy and stegochordy occur both in aquatic and burrowing forms such as ascaphids, discoglossids, pipids, rhinophrynids, and pelobatids. Contrariwise, holochordal or solid centra occur in almost all leaping, walking, and climbing terrestrial forms. Phylogenetically, the ectochordy and nonimbricate zygapophyses of Ramon frogs are replaced by stegochordy and imbricate zygapophyses in Recent pipids. Functionally, imbricate zygapophyses replace the centrum, which in the stegochordal condition merely links the bases of the neural arches (Griffiths, 1963). This evolution reflects the progressive adaptive improvement that pipids underwent in swimming efficiency. Evidently, ectochordy is primitive and preceded stegochordy and holochordy in anuran evolution. The first two central types typify the aquatic, the third one the terrestrial radiation of Anura.

Postsacrals. These are constantly present in Ramon frogs, in contrast to their infrequency in other anurans. *Thoraciliacus* has one, *Cordicephalus* two postsacrals as a

rule, though some individual variants display three and four urostylar vertebrae (Figs. 14, 15). One to three postsacrals may occur individually in Anura, particularly in the primitive families but also in some bufonids and ranids; but they are never a constant feature as in Ramon frogs. Recent adult pipids lack postsacrals, though three urostylar vertebrae are seen in premetamorphic *Xenopus* (Hodler, 1949; Smit, 1953). Thus pipids have eliminated postsacrals from the adult stage during their evolution, as did most frogs. This trend is linked to the basic adaptations of Anura and to the replacement of the undulatory by the propulsive type of locomotion, as registered in the short trunk and urostyle evolution. *Triadobatrachus* had an articulated tail involving at least six vertebrae (Hecht, 1962). Articulated tails have been reported in tadpoles of Recent *Megophrys major* (Griffiths, 1956) and of Ramon pipids (Nevo, 1956). These two finds register developmentally and paleontologically the evolution of the urostyle by fusion of caudal vertebrae [with a single hypochord in *Megophrys major* as demonstrated embryologically by Mookerjee (1931)]. Ramon frogs retain evidence of the primitive condition in both larva and adult. Gradual elimination of postsacrals through urostylization marks the transition from the undulatory proanuran to the propulsive anuran type of locomotion. The monocondylar sacro-urostylar joint of Ramon frogs distinguishes them from Recent pipids where this region is fused. The urostylar joint by itself has little taxonomic importance, yet it becomes significant within a character-complex. The region is functionally important, being free and flexible in leaping frogs (Whiting, 1961), but fused in aquatic forms "in which no shock absorption is required" (Green, 1931). Phylogenetically, the free joint preceded the fused region as the comparison of Ramon and Recent pipids shows. The same applies to fusions between ribs with their diapophyses or successive presacrals. Again, Ramon pipids usually have free ribs and free presacrals, whereas adult Recent pipids are ribless and have occasional presacral fusions. *Triadobatrachus* and all Mesozoic frogs have a monovertebral sacrum indicating the primitive condition. Synsacra, either in Recent or in Tertiary frogs, are specialized, and so are the expanded sacral diapophyses in aquatic and burrowing frogs.

Rib evolution in Anura is now traceable by means of fossils. Five ribs characterize premetamorphic paleobatrachids, and occur in individual specimens in 7.3 per cent of the *Thoraciliacus* sample (Figs. 14, 15). Four ribs occur in *Notobatrachus*, three Ramon species, and apparently also in *Saltenia* and *Shelania* (Casamiquela, personal communication). They may occur also in some individuals of *Xenopus* (Hodler, 1949). Three ribs are the rule in Recent costate anurans, but most Recent frogs are ribless. The long pipid ribs are points of insertion for muscles associated with the sub-aquatic locomotion which is to be discussed later. On the other hand, riblessness is at a premium in terrestrial anurans.

In sum, the column of *Cordicephalus* and *Thoraciliacus* is, in a broad sense, pipid, yet closer to ancestral conditions, differing from Recent pipids by a character-complex involving eight primitive as against two specialized characters (Table 10).

Pectoral girdle. The three Ramon species share essentially the same arciferal girdle, allowing for slight shape and size variations (see osteological summary and Fig. 12). They closely agree with the Recent pipids, particularly in the xenopoid pectoral girdle (De Villiers, 1924, 1929), in the following characters: *diverging coracoids and clavicles* (= arcifery *sensu* Cope and Boulenger); *a small scapula mostly uncleft proximally* (Proctor, 1921); *a large, V-shaped cleithrum, and episternum absent.* The Ramon girdles, particularly, approach the xenopoid type in having arched, anteriorly directed clavicles, shaft-like coracoids, and distinctly large cleithra. They are distinguished from *Xenopus* by having much

more arcuate clavicles, and coracoids more expanded at both ends, thus approaching the girdle of "eoxenopoidids" and paleobatrachids, e.g., the fossil pipoids.

Arcifery, small scapula and large cleithrum form an adaptive complex characterizing aquatic anurans. Arcifery is present in both aquatic and terrestrial anurans, but the association with a small scapula is exclusive to aquatic frogs. Small scapulae (clavicle to scapula ratio is greater than three) characterize pipids, ascaphids, and discoglossids. That ratio is less than two in all other (terrestrial) anurans and is probably to be correlated with the incorporation of the forelimbs into the active locomotory apparatus (Griffiths, 1963). It is noteworthy that *Hymenochirus*, the only firmisternal pipid, has also the relatively largest scapula in the family and is more terrestrial than the others (De Villiers, 1929), whereas some aquatic firmisternal forms (ranoids) have small scapulae (Hsiao, 1934). Further, a small scapula is typically associated with an uncleft proximal margin as in ascaphids and pipids. This is basically true for Ramon pipids, even though some ten per cent of the specimens have cleft scapulae (Fig. 14). Conversely, the long scapula is invariably cleft. *Triadobatrachus* and all known Mesozoic anurans share a small uncleft scapula. Thus the latter is primitive, and it appears to be associated with aquatic adaptation, whereas a long cleft scapula appears to be a terrestrial specialization.

Phylogenetically, arcifery appears to have preceded firmisterny, on the evidence of both the fossil record and comparative anatomy. *Triadobatrachus* had a pectoral girdle like that of *Ascaphus*, which is generally considered arciferal. All known Mesozoic frogs are probably in this sense arciferal. Reig's (1957) claim that *Notobatrachus* has a firmisternal pectoral girdle (and that hence that type is ancestral in Anura) was challenged by Eaton (1959) who compared it with the ascaphid girdle. In fact, all Recent primitive anurans are arciferal, whereas the advanced ranoids are firmisternal. The relatively large cleithra and clavicles of Ramon frogs are labyrinthodont characters and hence apparently primitive. De Villiers (1924, 1929) stressed the unique large cleithrum in *Xenopus*, and Aglossa generally, as opposed to the anterior small osseous seam in phaneroglossids. Regarding cleithrum size as of utmost importance in linking anurans and labyrinthodonts, he considered *Xenopus* more primitive than *Pipa*, partly on the ground of its larger cleithrum. Ramon pipids confirm his thesis. Lack of an episternum in *Triadobatrachus*, *Notobatrachus*, ascaphids and pipids, and its very small size in discoglossids indicate absence as a primitive feature.

The pectoral girdle of Ramon frogs is xenopoid and primitive both as a whole and as regards its six components (Table 10). The pipid girdle apparently has not changed significantly since early Cretaceous times and displays an ancestral aquatic adaptive-complex.

Pelvic girdle. All three Ramon species share a medium to long ischium and an *ossified* pubis; these features are indications of pipid affinities (Green, 1931, and his references). In other regards, the two Ramon genera differ basically in their pelves (Table 7). *Cordicephalus* approximates the xenopoid pelvis in its sacroiliac articulation, but lacks the epipubis. Conversely, *Thoraciliacus* matches "eoxenopoidids" in its medioiliac joint, but beyond that has an iliocostal contact in 83 per cent of the sample (Fig. 14), establishing a *functional* synsacrum.

Convergent origin of some anuran pelvic structures, such as an epipubis and synsacry, makes them unreliable taxonomic criteria at the familial level. The same, it appears to me, holds for the medioiliac articulation used as a diagnostic eoxenopoidid criterion (Casamiquela, 1961a). It has developed convergently in several lines, proves highly variable inter- and intraspecifically, and therefore is undiagnostic. Nor does it seem to be primitive, as contended

Table 7. Differences Between the Pelvis of *Cordicephalus* and *Thoraciliacus*

Genus	Shape of Pelvis	Sacroiliac joint	Ilium Length Head + Body Length*	
Cordicephalus	Triangular	Acroiliac No functional synsacrum	0.381	($N = 29$)
Thoraciliacus	Sub-parallel to triangular	Iliocostal or medioiliac Functional synsacrum	0.429	($N = 107$)

* Student's $t = 6.808$, for 134 degrees of freedom, $P < .001$.

by Reig (1957) and Casamiquela (1961a), but, rather, a specialized aquatic adaptation. Varied degrees of anterior iliac extension, or medioiliac articulation, show in some pipoids, such as eoxenopoidids, paleobatrachids, and *Thoraciliacus*, but not in others, e.g., *Cordicephalus* and Recent adult pipids. There is little indication of it in *Notobatrachus* and *Ascaphus*. The character has been reported for premetamorphosed and just metamorphosed *Rana temporaria* (Green, 1931) and similar stages in *Xenopus laevis* (Guardabassi, 1955; personal unpublished observations) but is not known for their adults. The character is extremely variable in *Thoraciliacus*, displaying varied degrees of anterior extension (Fig. 14), and a high V of 26.93 as against the average V of 18.05 (Fig. 16). The so-called "morphological stages" of *Eoxenopoides* (Haughton, 1931) seem to reflect individual variations similar to those in *Thoraciliacus* rather than progressive morphological series.

The medioiliac joint and expanded sacral diapophyses are explicable as an aquatic-burrowing adaptive complex. In *Xenopus* the sacroiliac joint is movable, the ilia slide freely backwards and forwards over the expanded sacral diapophyses, and the whole propulsive effort in swimming and burrowing occurs in one plane (Palmer, 1960). Whiting (1961) extended the principle of the movable sacroiliac joint to all frogs, showing that the region undergoes lateral and vertical bendings in climbing, walking, and jumping anurans, but longitudinal slidings in aquatic and burrowing forms. He suggested that in the pipids alternating lengthening and shortening of the trunk would increase the cycle, hence the stroke, of the hindlimb thrust. He further suggested that such an adaptation, involving expanded sacral diapophyses and sliding ilia, would be advantageous for burrowing anurans either in mud bottoms or on land.

Pipids are non-jumping, powerfully swimming anurans, burrowing occasionally underwater (Dunn, 1948; Johnson, 1952), presumably utilizing the Whiting-Palmer mechanism. I suggest that Ramon and other fossil pipoids employed the same type of movement. *Thoraciliacus* achieved one extreme by its labile functional synsacrum, which drastically shortened the column to just four free segments, eliminating the lateral movements and increasing propulsion. In having four functional, free, column segments, *Thoraciliacus* is different from any living or fossil vertebrate. It displays a highly specialized aquatic adaptation, a condition that would handicap terrestrial locomotion because of inability to bend at the sacroiliac joint. This suggests that *Thoraciliacus* inhabited the more open water, whereas *Cordicephalus* may have been a marginal dweller. Also, this unique specialization may have contributed to the extinction of the thoraciliacoid line in the changing environments of the Tertiary.

Ramon frogs thus appear to have a particularly specialized pelvis, especially so in *Thoraciliacus* (Table 10). The long ilia

of the anuran pelvis are a highly specialized phenomenon presumably present since the anuran grade was attained in the Triassic. The ossified pipid pubis is presumably specialized, since this element is cartilaginous in amphibamids, branchiosaurids, and *Triadobatrachus*. The alleged primitiveness of the medioiliac joint is questionable on several grounds: *Triadobatrachus* may have had anteriorly projecting ilia, though this is by no means clear. Anteriorly projecting ilia, however, are nonexistent or but little developed in Jurassic frogs; only later did this condition coexist with the normal sacroiliac joint, as evidenced by *Thoraciliacus* and *Cordicephalus* in the Cretaceous, and by paleobatrachids and xenopoids in the Tertiary. The feature is nonexistent or almost so in Recent adult pipids, discoglossids, and ascaphids. Its premetamorphic appearance in Recent unrelated frogs, as well as its prevalence among aquatic pipoids, suggest that it is paedomorphic in origin and a convergent aquatic specialization.

Limbs. The three species share most limb characters and vary but little. They agree broadly with the Recent pipid, particularly in the xenopoid manus and pes (osteological summary). All limb references, hereafter, for pipids, discoglossids, and pelobatids are to Howes and Ridewood (1888); for ascaphids to Stephenson (1952) and Ritland (1955).

Forelimb. Ramon frogs have the pipid manus pattern of four proximal carpals, inner centrale with a posterior spur, distal carpals aligned, and strikingly long metacarpals. In the latter feature they are sharply distinct from the discoglossids and ascaphids, which have short metacarpals. In carpal formula they approximate the eight of *Xenopus* rather than the six of *Pipa* or five of *Hymenochirus*, and in the diminishing order of finger length they are again like the former: 4-5-3-2. In totality, the manus is xenopoid-like with, however, an extra carpal. Ramon frogs retain the least modified anuran carpal formula, nine units including the prepollex carpal. Recent primitive anurans have eight free ossified carpals including the prepollex carpal. In adult discoglossids and pelobatids a vestige of the fifth proximal carpal appears, becoming ossified only in *Xenophrys*, the only hitherto known anuran with nine carpals. The fifth distal carpal of *Xenophrys* and of Ramon frogs corresponds to the fifth metacarpal, completing a distal carpal row of five including the prepollex.

Hindlimb. The Ramon frogs share with discoglossids and ascaphids the primitive pes condition of five distal tarsals. In this regard Ramon frogs depart from Recent pipids whose second or third distal tarsals are fused. *Cordicephalus* has an extra prehallux metatarsal which is absent in *Thoraciliacus*, but this is occasionally present along with additional phalanges in unrelated anurans, rendering it of little phylogenetic significance. The very long metatarsals and toes of Ramon frogs are as in other pipoids.

The limb similarities of Ramon frogs and *Xenopus* suggest an identity of function. The elongated fingers presumably compensate for tonguelessness in feeding, whereas the long apparently webbed toes provide powerful swimming oars. However, the pipid fore to hindlimb length ratio was significantly higher in Ramon than in Recent pipids. The ratio is 0.40 in *Hymenochirus*, 0.41 in *Xenopus*, and 0.47 in *Pipa*, whereas it is 0.56 in *Thoraciliacus*, and 0.59 in *Cordicephalus*. The higher Ramon ratio is evidently the primitive pipid condition which has decreased progressively to the low ratio of Recent pipids, which is presumably more adapted to aquatic life. Even the intergeneric difference in ratio of Ramon frogs is marginally significant (Student's $t = 2.124$; $p = 0.02$–0.05), suggesting that *Thoraciliacus* was more aquatic than *Cordicephalus*; this is in accord with the deduction from pelvic structure given above.

The presence in Ramon frogs of seven specialized and four primitive limb characters is shown in Table 10. Phylogeneti-

Table 8. Fossil Record of Mesozoic and Paleocene Frogs

Period	Family	Species	Horizon and Locality	Reference
JURASSIC:				
	Notobatrachidae	*Vieraella herbstii*	L.J., Patagonia	Reig (1961)
		Notobatrachus degiustoi	M.J., Patagonia, Argentina	Reig (1957) Casamiquela (1961 b)
	Discoglossidae?	*Eodiscoglossus santonjae*	U.J., Spain	Melendez (1957) Hecht (1963)
	[1]Pipidae?	*Eobatrachus agilis*	U.J., Wyoming, U.S.A.	Hecht and Estes (1960) Hecht (1963)
	Incertae sedis	*Comobatrachus aenigmaticus*	U.J., Wyoming, U.S.A.	Hecht and Estes (1960) Hecht (1963)
	Incertae sedis	*Montsechobatrachus gaudryi*	U.J., Spain	Hecht (1963, and references).
	?	*Stremmia scaber*	U.J., Africa	Hecht (1963, and references. He denies *Stremmia*'s anuran relationships).
CRETACEOUS:				
	Pipidae	*Thoraciliacus rostriceps*	L.C., Israel	Nevo (1964 b, and present study)
	Pipidae	*Cordicephalus gracilis*	L.C., Israel	" " "
	Pipidae	*Cordicephalus longicostatus*	L.C., Israel	" " "
	Leptodactylidae	Several still undetermined forms	L.C., Texas, U.S.A.	Hecht (1963, and references).
	"Eoxenopoididae"	*Eoxenopoides reuningi*	U.C.-L.E., South Africa	Haughton (1931) Casamiquela (1961 a)
	"Eoxenopoididae"	*Saltenia ibanezi*	[2]U.C.? Argentina	Reig (1959) Casamiquela (1961 a)
	"Eoxenopoididae"	*Shelania pasquali*	U.P.-L.E., Patagonia, Argentina	Casamiquela (1961 a, 1965).
	Ascaphidae?	Unidentified genus and species	U.C., Wyoming, U.S.A.	Estes (1964)
	Discoglossidae	Cf. *Barbourula* sp.	" "	" "
	Pelobatidae?		" "	" "
	Incertae sedis, near Hylidae?		" "	" "
	Incertae sedis, near Leptodactylidae?		" "	" "
	Other anuran remains, no family assignment		" "	" "

[1] The identification of *Eobatrachus agilis* as a pipid is tentative. Hecht (1963) remarks: "If *Eobatrachus* must be assigned to any family, it is most likely closer to the Pipidae." *Eobatrachus* has been defined from a humerus.

[2] Reig (1959) described *Saltenia* as a Lower Cretaceous form. Later evidence suggests probable Upper Cretaceous age (Casamiquela, personal communication).

L.J. = Lower Jurassic; M.J. = Middle Jurassic; U.J. = Upper Jurassic; L.C. = Lower Cretaceous; U.C. = Upper Cretaceous; U.P.-L.E. = Upper Paleocene-Lower Eocene.

cally, the fewer the fusions the more primitive the anuran carpus and tarsus; thus the nine carpals and five distal tarsals of Ramon pipids are distinctly primitive. Conversely, the long manus and pes, and fused radioulna and tibiofibula are specialized. Noteworthily, the branchiosaurs' 2, 2, 3, 3 finger formula, and the prevalent labyrinthodont 2, 2, 3, 4, 3 toe formula are present in most anurans, probably reflecting a primitive pattern.

In summary, the limbs of Ramon frogs match the xenopoid model but are more primitive in having an extra element in

both carpus and tarsus, and in their high fore- to hindlimb ratio.

Conclusions. The three Ramon species are assigned to the pipoids. They are highly variable in size, shape, and meristic characters. The first two sets of characters involve unresolved age and sex variations, the third set reflects individual variation. The types of meristic variations displayed by Ramon frogs are similar to those shown by other fossil and Recent anurans, though frequencies vary. *Thoraciliacus* is more variable than *Cordicephalus*, both in continuous and meristic variations. The highest variation in both genera is in the pelvis, the lowest in the limbs.

Ramon pipids involve a multiple-character basic adaptation to aquatic life. *Thoraciliacus* may have been more of a deep water, *Cordicephalus* more of a shallow water form. Thus, though certainly sympatric, they may have partly excluded each other competitively. Both suggest long progressive aquatic evolution of pipids. Presumably this started with emergence of the group in Triassic times and has continued ever since, at first rapidly and later at a slower rate. Aquatic adaptation was the principal factor involved in pipid origin and evolution.

Ramon pipids show a melange of 21 primitive versus 16 specialized characters. They attest to the common rule that in a given sequence no one taxon will be more primitive than others in all respects. Yet the skull, pelvis, and limbs are essentially specialized, whereas the vertebral column and pectoral girdle are mainly primitive. The two Ramon genera are the most primitive pipids yet known. *Cordicephalus* is more primitive than *Thoraciliacus*.

The Systematic Position of *Cordicephalus* and *Thoraciliacus* and Remarks on Pipoid Classification

Detailed analysis unequivocally shows the pipoid affinities of Ramon frogs but does not immediately settle their familial allocation. In fact, pipoid classification is far from settled, as is clear from recent suggested revisions of the Pipidae (Dunn, 1948; Lamotte, 1963), and pipoids (Reig, 1958; Casamiquela, 1961a) and the problematic relationships of paleobatrachids (Hecht, 1963) and rhinophrynids (Orton, 1953, 1957). Three problems are involved: (a) ranking of the lower categories within Pipidae; (b) vertical versus horizontal classification (or how to classify fossil pipoids); and (c) significance of larvae in anuran classification (or rhinophrynid relationships). The solutions to these taxonomic problems depend on evaluation of pipoid classification, the fossil record, and tadpoles.

Classification of Recent pipids. In 1830 Wagler introduced the primary divisions Aglossa and Phaneroglossa. The former has been considered taxonomically valid ever since, despite much shifting of its categorical rank (see Griffiths, 1963, for historical review). Recent studies make obsolete the African *Xenopinae* and South American *Pipinae*, recognized by Noble (1931), since the differences "cannot be considered of more than generic value" (Dunn, 1948). African *Hymenochirus* is closer to American *Pipa* than to African *Xenopus*, as evidenced by comparing the skulls (Paterson, 1945), pectoral girdles (De Villiers, 1929), and vertebral columns (Boulenger, 1899). Furthermore, Dunn regarded the three South American genera *Pipa*, *Protopipa*, and *Hemipipa* as merely three species of *Pipa*. Lamotte (1963) regards *Pseudohymenochirus* as a subgenus of *Hymenochirus*. Accordingly, the purely aquatic Recent Pipidae comprise three genera: the South American *Pipa*, with five species; African *Xenopus*, five species; and *Hymenochirus*, five species.

The Recent Pipidae, the sole family of Aglossa, are characterized by: tonguelessness, a single median opening to the eustachian tubes, azygous frontoparietals, absence of a maxillary arcade (= no quadratojugals), greatly expanded sacral diapophyses, sacrum fused to urostyle, three free

TABLE 9. OSTEOLOGICAL COMPARISONS AMONG PIPOID GENERA, FOSSIL AND RECENT

Character	RAMON PIPIDS		"EOXENOPOIDIDAE"			PIPIDAE			PALAEOBATRACHIDAE	Rank of Character
	Cordicephalus	*Thoraciliacus*	*Eoxenopoides*	*Saltenia*	*Shelania*	*Xenopus*	*Hymenochirus*	*Pipa*	*Palaeobatrachus*	
SKULL:										
Maxillary arcade incomplete	+	+	+	+	+	+	+	+	+	Superfamilial
Frontoparietals azygous	+	+	+Suture	+Suture	+Suture	+	+	+	+	Superfamilial
Maxillae and premaxillae dentigerous (D) or edentulous (E)	D	D	E	?	E	D	E	E	D	Generic
Quadratojugals absent	+	+	+	+	+	+	+	+	+	Superfamilial
Palatines absent	+	+	+	+	+	+	+	+	+	Superfamilial
Mentomandibulars absent	+	+	?	?	?	+	+	+	?	Familial?
Squamosals reduced	+	+	+	+	+	+	+	+	+	Superfamilial
Pterygoid large	+	+	+	?	?	+	+	+	+	Superfamilial
Otic capsules large	+	+	+	+	+	+	+	+	+	Superfamilial
Columella present	+	+	?	+	?	+	+	+	+	Superfamilial
Parasphenoid: sword-like (S), dagger-like (D), broad (B)	S	S	D	?	B	S	B	B	D	Generic
Nasals: broad (B), narrow (N), medium (M)	M	B	B	B?	B	N	B	B	B	Generic
Mandible edentulous	+	+	+	+	+	+	+	+	+	Superfamilial
VERTEBRAL COLUMN:										
Presacral vertebrae	8	8	6–7	8	8	8	6	7	7	Generic
Sacrum composed of the following vertebrae:	9th	9th	9th	9th	9th	9th	7th+ 8th+ 9th	8th+ 9th	7th+ 8th+ 9th	Generic
Expanded sacral diapophyses	+	+	+	+	+	+	+	+	+	Superfamilial
Postsacral vertebrae in adults	2(1)	1	0	0	0	0	0	0	0	Generic
Vertebral articulation: opisthocoely (OP), procoely (PR)	OP	OP	OP	OP	OP	OP	OP	OP	PR	Familial
Ribs in adults: free, or fused	Free	Free	Fused?	?	Free	Fused	Fused	Fused	Fused	Generic
Sacro-urostylar articulation: synostotic (S), monocondylar (M), bicondylar (B)	M	M	S	S	S	S	S	S	B	Generic
Fusion of presacrals	—	—	—	—	—	+	+	+	+	Generic
PECTORAL GIRDLE:										
Type: arciferal (A), firmisternal (F)	A	A	A	A	A	A	F	A	A	Generic
Coracoids: narrow (N), broad (B)	N	N	N	N	N	N	B	B	N	Generic

TABLE 9. *Continued*

Character	RAMON PIPIDS		"EOXENOPOIDIDAE"			PIPIDAE			PALAEOBATRACHIDAE	Rank of Character
	Cordicephalus	*Thoraciliacus*	*Eoxenopoides*	*Saltenia*	*Shelania*	*Xenopus*	*Hymenochirus*	*Pipa*	*Palaeobatrachus*	
Clavicles: arched (A), straight (S)	A	A	A	A	A	A	S	S	A	Generic
Scapula small uncleft	+ +	+ +	+ ?	?	+ ?	+ +	+ +	+ +	+ +	Superfamilial
Cleithrum V-shaped	+ +	+ +	+ ?	?	?	+ +	+ +	+ +	+ +	Superfamilial
PELVIC GIRDLE:										
Pubis ossified	+	+	+	?	?	+	+	+	+	Superfamilial
Sacroiliac articulation: medioiliac (M), acroiliac (A)	A	M	M	M	M	A	A	A	M	Generic
LIMBS:										
Four long metacarpals	+	+	+	+	+	+	+	+	+	Superfamilial
Distal tarsals	5	5	?	?	?	4	4	4	?	Generic
Five long metatarsals	+	+	+	+	+	+	+	+	+	Superfamilial

larval ribs, basic arcifery, small uncleft scapula, large V-shaped cleithrum, and elongated metatarsals and metacarpals.

Classification of fossil pipoids. Classification of fossils always poses the alternative of horizontal versus vertical classification. The first emphasizes the uniqueness in space and time of contemporaneous related taxa; the second stresses ancestor descendant relationships of successive taxa. Should Cretaceous pipoids, the Ramon ones included, be allocated to a separate family, or assigned to Recent Pipidae?

Casamiquela (1961a), following a suggestion of Reig (1958), preferred the first alternative and established the *Eoxenopoididae*, to accommodate *Eoxenopoides*, *Shelania*, and *Saltenia* (Table 8) from the Cretaceous and Paleocene of Africa and Argentina. He brigaded *Eoxenopoididae* with *Pipidae* and *Paleobatrachidae* in the suborder Aglossa *sensu* Reig (1958) and defined the new family as having: (1) an ovoid skull; (2) a quadratojugal arch absent; (3) rhomboid frontoparietals, joined in a sagittal depression and having a longitudinal suture; (4) large otic capsules; (5) narrow styliform coracoids; (6) opisthocoelous vertebrae; (7) sacrum fused with urostyle; (8) greatly expanded sacral diapophyses, articulating with the middle portion of the ilia; and (9) hindlimb larger than forelimb.

Of those nine diagnostic characters, six are shared with Pipidae and just three (3, 4, 8) are novel. Yet all three, evaluated above, are seen to fall within individual, age, and intergeneric variations of Recent Pipidae and of *Thoraciliacus* and hence are not suitable to diagnose a new family. Even taken together they fail to show the clearly defined gap which would justify a new pipoid family. A split such as this ignores the great skeletal variation displayed by Recent pipids, which shows arcifery and firmisterny, mono- and synsacry, five to eight presacrals, and great size and shape variations. Likewise, the medioiliac joint should be considered variable in

Table 10. Primitive Versus Specialized Characters in Ramon Pipids

Character	Primitive	Specialized
SKULL:		
Rostrum		+
Azygous frontoparietals		+
Large otic capsules		+
Absence of palatines, quadratojugals, and mentomandibulars		+
Reduced squamosals and maxillae		++
Dentigerous maxillae and premaxillae	+	
Plectrum of columella	+	
Ossified quadrate	+	
VERTEBRAL COLUMN:		
Eight presacral vertebrae	+	
Postsacral vertebrae	+	
Ectochordal centrum	+	
Opisthocoely	+	
No presacral fusions	+	
Free monocondylar sacro-urostylar articulation	+	
Four free ribs	+	
Monovertebral sacrum	+	
Expanded sacral diapophyses		+
Diapophyses of presacrals 6–8		+
PECTORAL GIRDLE:		
Arcifery	+	
Large clavicles	+	
Uncleft scapula	+	
Small scapula	+	
Large cleithrum	+	
No sternum, episternum, or coracoidal cartilages	+	
PELVIC GIRDLE:		
Functional synsacrum in *Thoraciliacus*		+
Ossified pubis		+
FORE LIMB:		
Developed capitate eminence		+
Developed olecranon		+
Very long metacarpals		+
Nine carpals	+	
Phalangeal formula 2, 2, 3, 3,	+	
Pointed terminal phalanges		+
HIND LIMB:		
Five distal tarsals	+	
Very long metatarsals		+
Phalangeal formula 2, 2, 3, 4, 3	+	
Pointed terminal phalanges		+

pipoids or, alternatively, *Cordicephalus* and *Thoraciliacus* should be assigned to separate families, despite all the weighty evidence that admits only a generic level of separation.

The characters distinguishing Ramon from Recent pipids, e.g. four ribs, regular presence of postsacrals, and a free sacro-urostylar joint, are certainly primitive. Yet they appear to be inappropriate as taxonomic criteria at the family level, as do eoxenopoidid characters. I suggest that eoxenopoidids and Ramon pipoids, on the contrary, be allocated to the Pipidae, which then must be slightly redefined to allow for free ribs, a sacro-urostyle joint, and postsacrals in adults. This solution would be in accord with recent lumping trends in Recent pipid classification (Dunn, 1948). Further, it will fit the general taxonomic postulate that genera tend to be horizontal, families vertical categories (Simpson, 1961). The Pipidae are a natural group embracing varied forms, but the differences between known Cretaceous and Recent pipoids cannot, I think, be considered of more than generic rank.

Other pipoids and their supposed relatives should now be briefly mentioned. The classification and relationships of the Tertiary European paleobatrachids has long been debated. They have been considered Aglossa (Špinar, 1963, and references), or as convergent to the Aglossa (Noble, 1931), or unnatural, comprising several families (Hecht, 1963). Recent studies of rich new material have led Špinar (1963) to confirm the taxonomic validity and pipoid affinities of paleobatrachids. He has revised the family, recognizing two genera and five species, and has redefined it as having seven procoelous presacrals, synsacry, five free larval ribs, fusion of presacrals 1–2, and a bicondylar sacro-urostylar joint. Pipid affinities are suggested by an incomplete maxillary arcade, azygous frontoparietals, ossified pubis, arcifery, elongated manus and pes, and five free larval ribs.

Kuhn (1941) described the genus *Opisthocoelellus* from the middle Eocene of Geiseltale, Germany, associating it with *Eoxenopoides*, and later placed it in a separate family. Hecht (1963), re-examining the material, could recognize no form ascribable to pipids.

The significance of the pipid larva, or rhinophrynid relationships.[1] Rhinophrynids have proved problematical; they were first affiliated with bufonids (Noble, 1931), later on with pipids (Orton, 1953, 1957) on the morphology of the tadpole. Griffiths (1963) has questioned the validity of basing major phylogenetic conclusions in Anura on larval characters alone. I have suggested elsewhere (Nevo, MS) that Recent pipid tadpoles are secondarily simplified, rather than primitive, basing my inferences on the sole known Cretaceous pipid tadpole (Nevo, 1956). The same suggestion, based on other grounds, was made by Tihen (1965); he, however, accepts pipid-rhinophrynid relationships on grounds of both larval and adult evidence. Adult rhinophrynids unquestionably display a mixture of primitive and specialized characters (Walker, 1938). Their primitiveness is explicit in ectochordy, large cleithrum (Meszoely, 1966), amphicoely[2] and eight carpals (personal observations). They are specialized in having a bicondylar sacro-urostyle joint, in being ribless in all stages, in their long cleft scapula, type of hyolarynx, neural arches, and limbs. Neither the primitive nor the specialized characters, it appears to me, imply pipid affinities. The former suggest ancestral proanuran, the latter terrestrial burrowing characters. Some skull characters do show similarity to pipids (Tihen, 1965; Meszoely, 1966), but others such as the complete maxillary arcade, absence of a columella, small pterygoids, and well-developed squamosals, are non-pipid. Also, postcranially, they differ from pipids in the primitive and specialized characters mentioned. All in all, I think that rhinophrynids are mosaics of primitive, basically proanuran characters, and characters specialized for burrowing, rather than pipid relatives. Both probably evolved directly from a proanuran stock into different adaptive zones, rhinophrynids into the burrowing zone, pipids into the aquatic zone.

In summary, taxonomically, pipoids comprise the Pipidae and Paleobatrachidae. The former, with a slight expansion of its definition, may appropriately accommodate both Recent and all known Cretaceous pipoids.

Pipoid Evolution

General. The evolutionary status and origin of pipids have proved problematical ever since their recognition, in contrast to their taxonomic stability. They were considered as either primitive (Noble, 1922) or specialized (Ryke, 1953, and references), and variously derived (see later). Several factors have obscured the phylogenetic status and derivation of pipids: (a) description in extreme antithetical terms as *either* primitive *or* specialized; (b) their strong and basic aquatic adaptation; (c) absence until recently of knowledge of any fossil record.

As is true of other taxa, any attempt to regard pipids as altogether primitive or specialized is doomed to failure. Pipids showed a melange of primitive and specialized characters even by early Cretaceous times (Table 10), although the specialization has, of course, increased in Recent pipids. Some of their primitive skeletal characters have long been understood as such (opisthocoely, larval ribs, large cleithra, small uncleft scapula, etc.). Conversely, long recognized specializations are the long manus and pes, loss and reduction of skull bones, vertebral fusions, etc.

[1] I am grateful to Mr. Charles Meszoely, who permitted me to examine the rhinophrynid skeletons he is studying.

[2] Walker (1938: 2) describes the vertebrae as opisthocoelous, but in his discussion (pp. 8–9) he compares them with ascaphid vertebrae, e.g. ectochordal and amphicoelus. Tihen (1965) regards them as opisthocoelous.

In the literature of the group, neoteny is probably the most strongly emphasized pipid characteristic. It has been considered the basic evolutionary factor in their history (De Villiers, 1934). Thus all pipid specializations have been attributed to neoteny (Millard, 1949; Ryke, 1953), which has been described as the "only common factor of this polyphyletic group" (De Villiers, 1963, personal communication). The neotenic hypothesis implies that pipids are secondarily aquatic and have regained their lateral line organs through neoteny. This hypothesis is thus not valid if pipids originated in water and have retained their primary lateral line organs (Grobbelaar, 1925). Moreover, the aquatic hypothesis stresses the *basic adaptation* involved in the origin and development of pipids rather than the specific operating *genetic mechanism*. The question, at all events, is one for which knowledge of the early environment of anurans as a whole is crucial.

Early environment and the evolutionary basis of pipids. The period of transition from proanurans to anurans is as yet undocumented by fossils. Hypotheses have been advanced for an (a) aquatic (Böker, 1935; Griffiths, 1963), (b) terrestrial (Inger, 1962), and (c) riparian (Gans and Parsons, 1966, and references) origin of frogs. The fossil evidence available suggests a probable aquatic origin. Neither *Triadobatrachus*, the probable ancestor (Griffiths, 1963), nor its Jurassic frog descendants are conceivable as terrestrials. The early true frogs, involving mainly ascaphids, discoglossids and pipids, with ecto- and stegochordy, amphi- and opisthocoely, arcifery and small scapula, present a character-complex incompatible with terrestrial life. The earliest terrestrial frogs known from the Cretaceous present holochordy, basic procoely, and long scapulae.

The concept of pre-frogs as aquatic is neither contradictory of nor incompatible with the idea of the jumping mechanism in frogs evolving while they were also using undulatory locomotion (Griffiths, 1963). Since, functionally, swimming and jumping are not incompatible (Gans and Parsons, 1966), it is conceivable that the propulsive thrust mechanism could have evolved in basically aquatic animals. It might have had the same selective advantages in water and riparian habitats, either as a means of catching food more efficiently, or of escaping from predators into mud bottoms and vegetation, or from bank into water.

The evidence of early Cretaceous pipids attests that Recent pipids have carried forward an aquatic adaptation of ancient origin, and perfection of this adaptation most probably operated as the main evolutionary selective factor since the origin of the taxon. This process has had multiple effects on the skeleton, making pipids very much water-adapted stereotypes throughout their evolution. If this thesis is true, then neither neoteny nor the potentiality of lateral line reappearance upon reinvasion of water (Escher, 1925) is necessary to account for pipid evolution.

The thesis advocating aquatic evolution of pipids stresses a *process* of progressive adaptation for the development of the taxon rather than the genetic *mechanism*(s) involved. Neoteny is neither genetically different nor more important than other ontogenetic processes involving genetic change (Simpson, 1953, and Rensch, 1960, have thoroughly evaluated the role which neoteny has played in evolution). Some probable paedomorphic characters exhibited by pipid skulls or pelves by no means violate the basis of this thesis. They presumably resulted from mutations affecting early stages of development. Other characters, including probably the majority of aquatic adaptations such as elongated manus and pes and expanded sacral diapophyses, are due to mutations affecting late ontogenetic changes.

The evolutionary interpretation of pipids is meaningful only in terms of progressive *aquatic adaptation* since their origin, probably in the Triassic. This thesis is borne out, at least inferentially, by Ramon pipids.

Phylogeny. Pipids were phylogenetically derived from: (a) discoglossids (Noble, 1925); (b) proanuran stock (De Villiers, 1929); (c) "widespread group of Anura" in late Triassic-early Jurassic times (Hecht, 1963); (d) a pipoid stem stock from which all non-ascaphid forms originated (Griffiths, 1963). Views (a), (b), and (d) are based mainly on comparative anatomy grounds, while (c) partly hinges on Orton's (1953) tadpole studies. All these views were handicapped by the scanty pipid fossil material available at the time they were proposed, yet all share the belief in *early* pipid derivation. This conception is borne out by the fossil record, which suggests to me a direct derivation of pipids from proanurans. The independent existence in the Jurassic of ascaphids, pipids, discoglossids, and possibly some representatives of the advanced frogs, favors the view of basal rapid diversification of those lines from proanurans in the Triassic; the crucial story of the transition period remains to be told.

Pipid phylogeny as conceived by this study is shown in Figure 17. The earliest known certain pipids are *Cordicephalus* and *Thoraciliacus*. Both suggest a long Jurassic evolution and probably early diversification. The cordicephaloid line, the more primitive of the two, evolved slowly into the xenopoid line in the Tertiary. The Recent genus *Xenopus*, a direct derivative of this line, is known from the Miocene of Africa (Ahl, 1926). The thoraciliacoid line, on the other hand, exhibits high aquatic specializations, particularly in the pelvis. This rapidly evolving line culminated in Cretaceous-early Tertiary times in forms like *Saltenia* and *Shelania* in South America, and *Eoxenopoides* in South Africa, thereafter becoming extinct. The paleobatrachids, apparently an independent pipoid line whose relationships and origin are still obscure, flourished for a short time in Europe during the Tertiary, becoming extinct in late Miocene times. *Pipa* and *Hymenochirus* whose direct ancestry is yet undocumented, presumably originated like *Xenopus* in the early Tertiary, while Recent species are probably late Tertiary-Pleistocene derivatives.

The overall similarities between *Cordicephalus* and Recent *Xenopus* suggest relatively slow evolutionary rates for this line during the Cenozoic. Yet structural improvements in aquatic adaptations have occurred since the Cretaceous and will be discussed below. Taxonomic diversification has presumably been limited in pipids throughout their history. Neither the three extant genera, with 15 species, nor the handful of known Cretaceous genera suggest a high level of taxonomic proliferation. However, the extinction of several pipid lines during the Tertiary may suggest somewhat higher early diversification.

Evolutionary trends. Pipids show a basic broad aquatic adaptation that has gradually improved; this is evident from comparing Ramon and Recent pipids (Table 9). The skeletal improvements involve fusions, losses, reductions, changes in ratios, increase in size, and drastic larval changes.

The vertebrae evolved from ectochordal to stegochordal, and the neural arches became imbricate. Postsacrals in adults were eliminated, and the urostyle fused to the sacrum. Fusions occurred in adults between ribs and their diapophyses, between some successive vertebrae, between carpals, and between distal tarsals. In *Pipa* and *Hymenochirus*, the number of presacrals was reduced by fusions to seven and six, respectively, and in both the teeth were lost. Skeletal ratios significantly changed; foremost among these was the change in length ratio of fore- to hindlimb from 0.59 in Cretaceous *Cordicephalus* to 0.40 in Recent *Xenopus*. *Hymenochirus* turned firmisternal and developed synsacry, thereby shortening its column to just five free segments. A phyletic increase in size is probable in pipids, particularly in the line leading from *Cordicephalus* to *Xenopus*, a trend indicated in many other phyletic lines by "Cope's Rule."

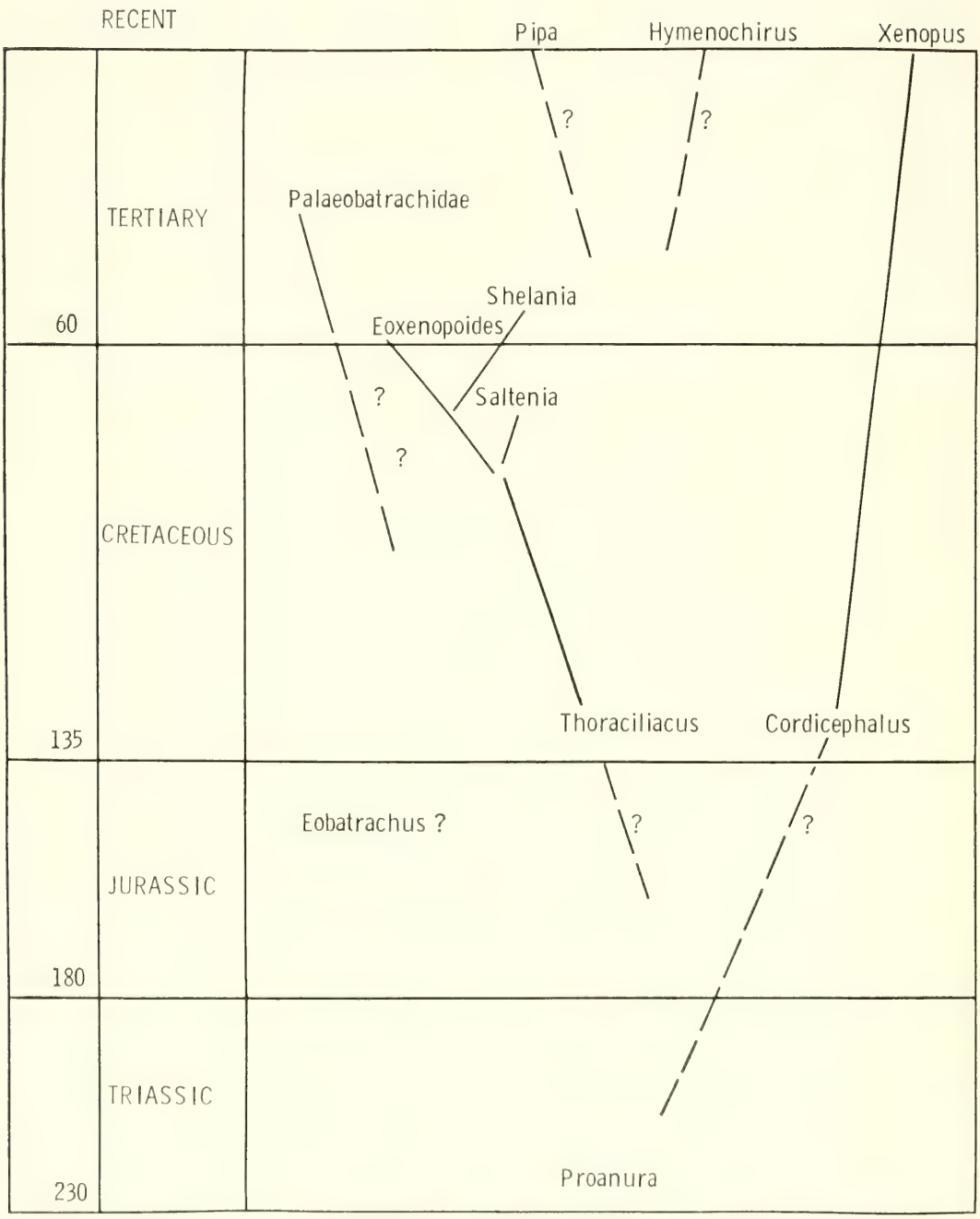


Figure 17. Diagram illustrating relationships of pipoids as suggested by this study, plotted against time scale. Continuous lines based on available fossil record; broken lines hypothetical. Left column indicates approximate time since the beginning of the periods in million of years.

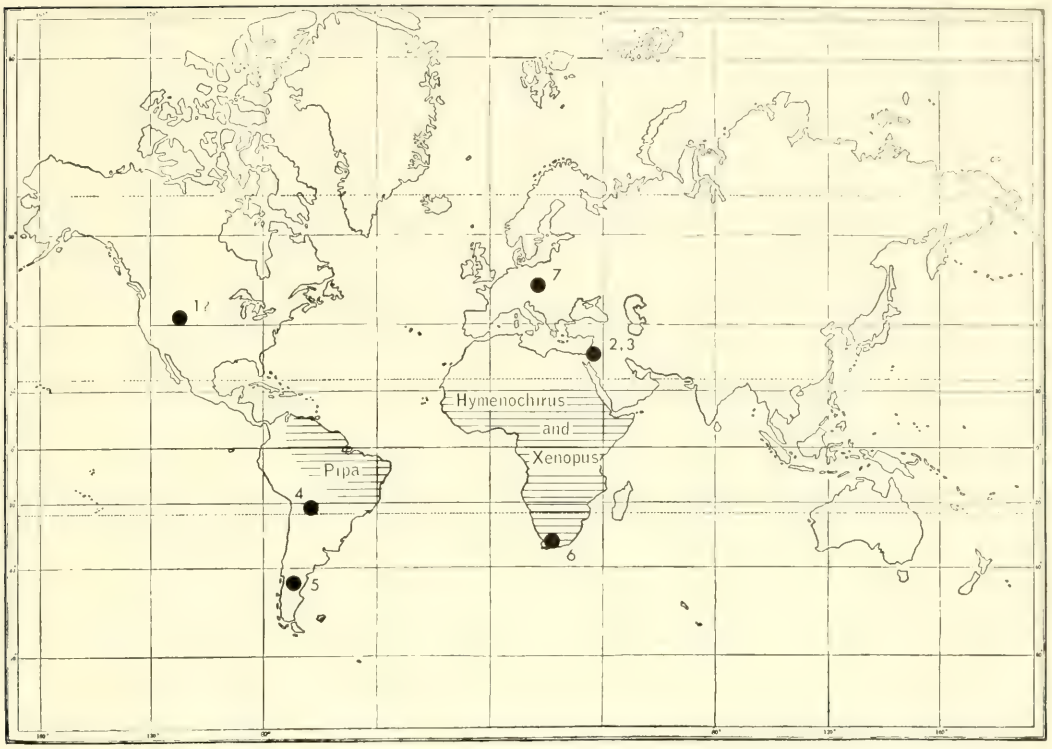


Figure 18. The distribution of Recent and fossil pipoids. Recent pipids are indicated by horizontal lines: in South America—*Pipa*; in Africa—*Xenopus* and *Hymenochirus*. Fossil pipoids are indicated by numbered circles: 1. *Eobatrachus agilis*; 2, 3, *Thoraciliacus* and *Cordicephalus*; 4. *Saltenia ibanezi*; 5. *Shelania pasquali* 6. *Eoxenopoides reuningi* and *Xenopus stromeri*; 7. *Palaeobatrachidae*.

The most impressive modification pipids underwent is in the evolution of their larvae. Their ancestral larva had tail vertebrae (Nevo, 1956) as in the Recent *Megophrys major* (Griffiths, 1956). Paleobatrachids had normal tadpoles without caudal vertebrae in the Miocene. If this reflects the condition of the contemporaneous pipid larva in the Tertiary, then the change from the ancestral to the present secondarily simplified larva occurred in late Cretaceous-early Tertiary times.

Paleogeography. The distribution of Recent and fossil pipoids is shown in Figure 18. At present, pipids have a disjunct distribution, mostly in the tropics of the old and new worlds. This pattern is a remnant of a pipid distribution over the greater part of the world during Cretaceous times, possibly extending back into the Jurassic, as suggested by the fossil record. The ever changing, often contradictory views on anuran centers of origin and dispersal routes testify to the near impossibility of a sound zoogeography unless documented by fossils. Furthermore, even the fossil record, which is rare and accidental in frogs, particularly in terrestrial ones, may be misleading unless it is documented by evidence of early radiations. In frogs such radiations presumably occurred in the Triassic, and are as yet undocumented.

The history of fossil pipoid discoveries illustrates perfectly how postulates of place and time of origin are directly related to successive fossil finds. The rich paleobatrachid finds early in the last century, from the Tertiary of Europe, added support to

the Holarctic school advocating a northern origin of Anura (Noble, 1931). The Cretaceous *Eoxenopoides* from South Africa supported the postulate, based mainly on the distribution of modern forms, that the Old World tropics was the sought-for center (Darlington, 1957). The subsequent discoveries of *Saltenia* and *Shelania* from the Cretaceous and Paleocene of Argentina, plus the Jurassic *Notobatrachus*, suggested South America as the pipoid center of origin (Casamiquela, 1961a). Similar logic might now suggest Asia as the pipid center, based on Ramon pipids. Evidently, however, the crucial discoveries which will elucidate centers of origin of pipids and other early frog lineages are yet to be made in continental Triassic rocks.

SUMMARY AND CONCLUSIONS

1. The fossil record of frogs is more complete than has been realized, particularly for pipids, and must be considered in evolutionary interpretations along with studies of Recent forms.
2. The Ramon frog collection permits studies of the whole skeleton of great numbers. Consequently, it enables population studies of inter- and intraspecific variations, population dynamics, adaptive complex, and phylogenetic interpretation.
3. All Cretaceous pipoids may be referred to Recent Pipidae.
4. The evidence of Ramon and other Cretaceous pipids suggests that:
   (a) Pipids have been an independent aquatic line, at least since the Jurassic, and they probably were derived directly from proanurans in Triassic times.
   (b) Pipids are primarily aquatic; their origin and evolution involve a basic aquatic adaptive complex progressively improving in aquatic co-adaptation.
   (c) Pipids are, and have always been, a melange of ancestral and specialized characters, yet the latter proportionately increase in time. The skull, pelvis, and limbs specialized early in pipid evolution, whereas the column and pectoral girdle always lagged behind.
   (d) Evolutionary trends in the pipid skeleton involve structural changes, fusions, losses, reductions, ratio changes, and increase in size. Most are explicable as improvements in aquatic adaptation.
   (e) Pipids have probably never been taxonomically prolific, yet their record suggests a rapid basal limited diversification, then some Tertiary extinctions, and later a slower generic and specific splitting in the Tertiary.
   (f) The cordicephalid line appears to be ancestral to the xenopid; the thoraciliacid line is related to "eoxenopoidids," but became extinct in Tertiary times.
   (g) Pipids had an almost worldwide distribution in the Cretaceous and probably in late Jurassic times; their center of origin is as yet unknown.

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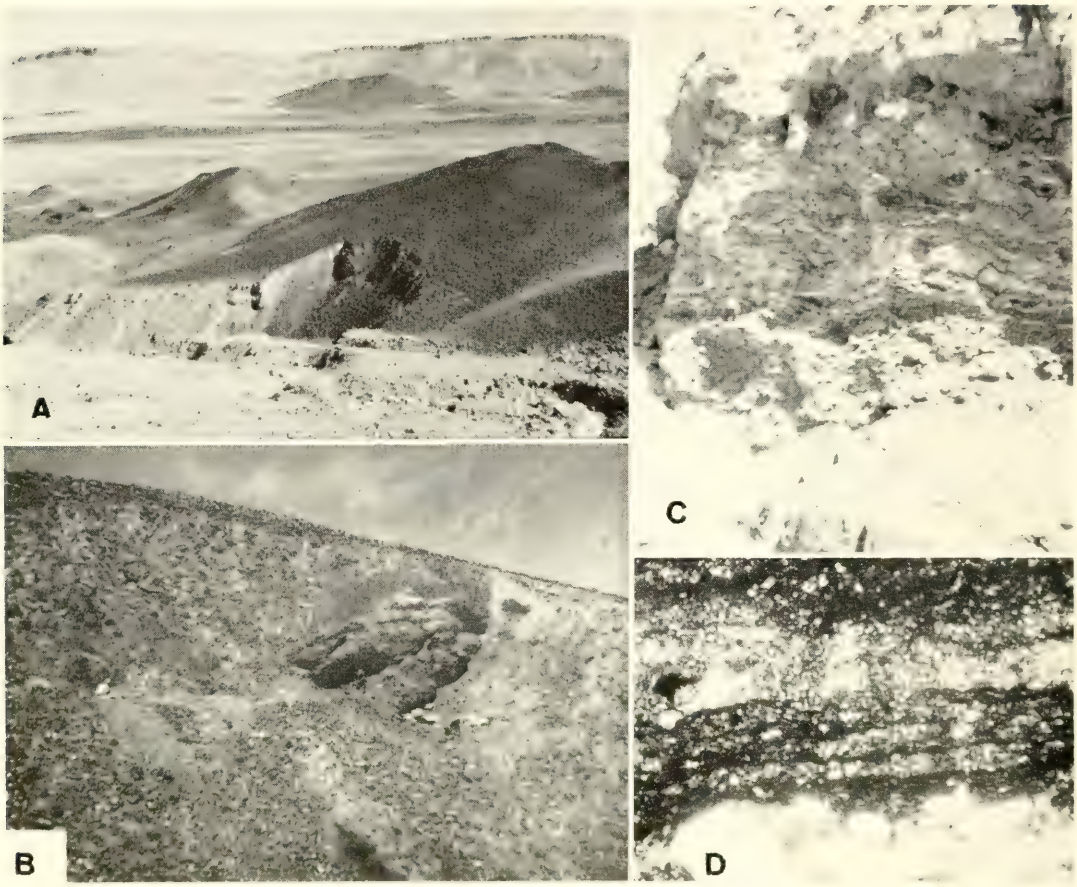

Plate 1. The Amphibian Hill locality in western Makhtesh Ramon, Israel.

A. Regional view of western Makhtesh Ramon. The rim is made up of Cenomanian formations, overlying the Nubian Sandstone which forms the slope. The black hills are composed of the upper and lower basalts of early Cretaceous age. The black basalt hill in the right half of the photograph is the Amphibian Hill comprising the exposure from which all the frog collection has been dug. This exposure is progressively enlarged by increasing closeups in Figures B, C, and D.

B. The silt unit comprising the frogs is seen as a tilted lens overlying the lower basalt and underlying the upper basalt. The lens tapers out under the basalt cover.

C. A closeup of the amphibian bed, showing the laminated deposit.

D. A thin section of the rock comprising the frog bed, magnified × 30. Note the white laminations consisting of quartz grains and alternating with the black hematitic-limonitic laminae which contain the fossil frogs.

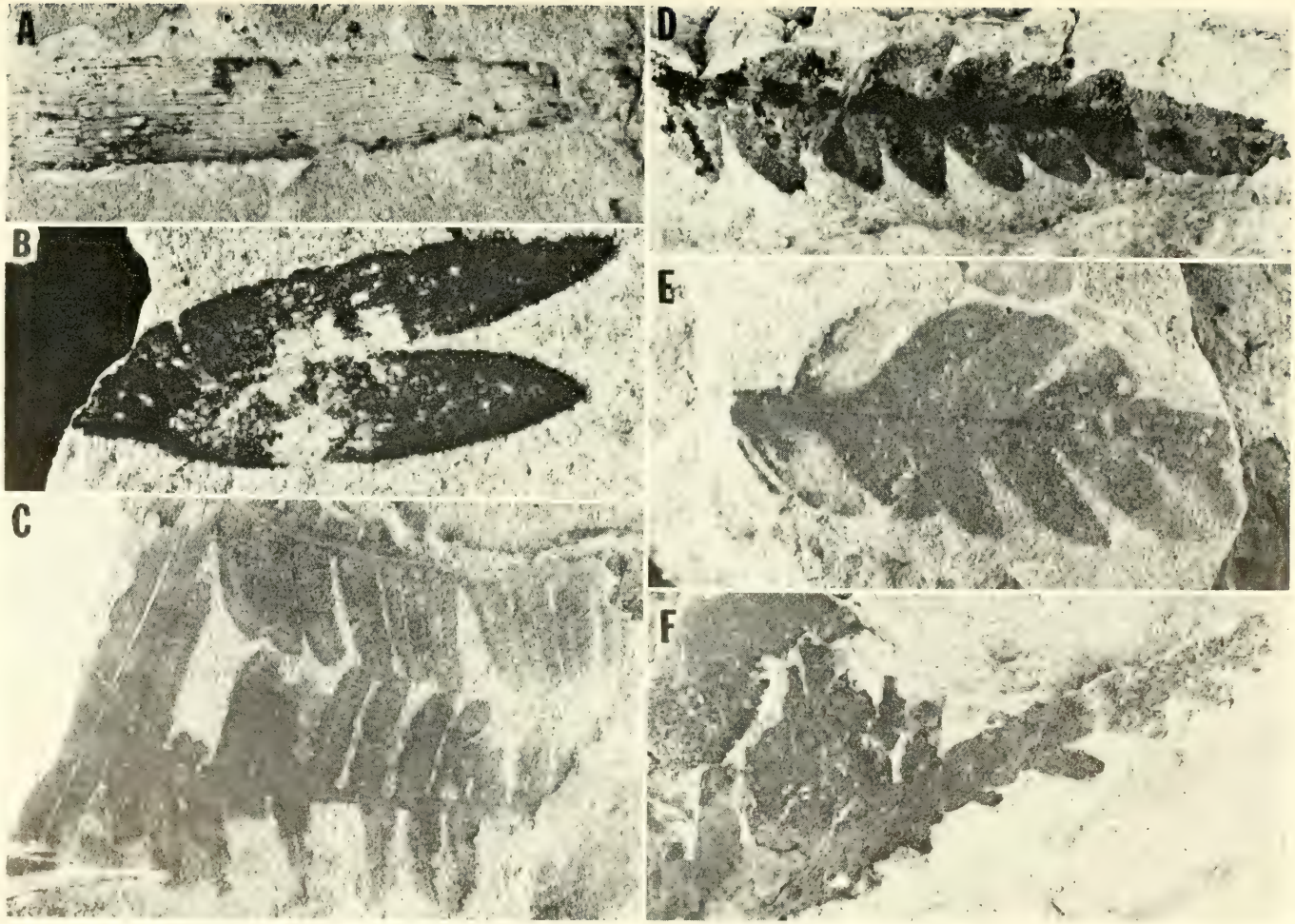

Plate 2. Lower Cretaceous fossil plants from the amphibian bed, Makhtesh Ramon. A. *Podozamites* sp.; B. *Schizolepis* sp.; C. *Phlebopteris tertile* ?; D. *Cladophlebis* sp. E. *Cladophlebis* sp.; F. *Brachyphyllum obesum*. (Identification of plants was kindly provided by Dr. J. Lorch, Department of Botany, Hebrew University, Jerusalem.)

Plate 3. *Thoraciliacus rostriceps* n.g., n. sp., early Cretaceous, Makhtesh Ramon, Israel. All specimens of the species were collected from the same deposit, shown on Plate 1, fig. C, magnified × 3. All are deposited in the Hebrew University, Jerusalem, Department of Zoology, abbreviated to HUJZ. A. Type specimen, HUJZ, F 93; compare with drawing of Figure 4. B. HUJZ, F 85; an almost complete specimen showing most of the species characteristics.

Plate 4. *Thoraciliacus rostriceps*, magnified × 3. A. HUJZ, F 70 b. Note details of skull, scapula, ribs, anterior ilia and postsacral vertebra. B. HUJZ, F 40. Note dentigerous premaxillae and maxillae, parasphenoid, coracoid, four free ribs, postsacral vertebra, and hour-glass effect in presacrals.

Plate 5. *Thoraciliacus rostriceps*. A. HUJZ, F 12; note azygous frontoparietals, incomplete dentigerous maxillary arcade, extensive otic capsules, four ribs, mediolliac articulation, carpals. B. HUJZ, F 110 b; note elongated manus and pes. C. HUJZ, F 124; note complete pectoral girdle and anteriorly extended ilia.

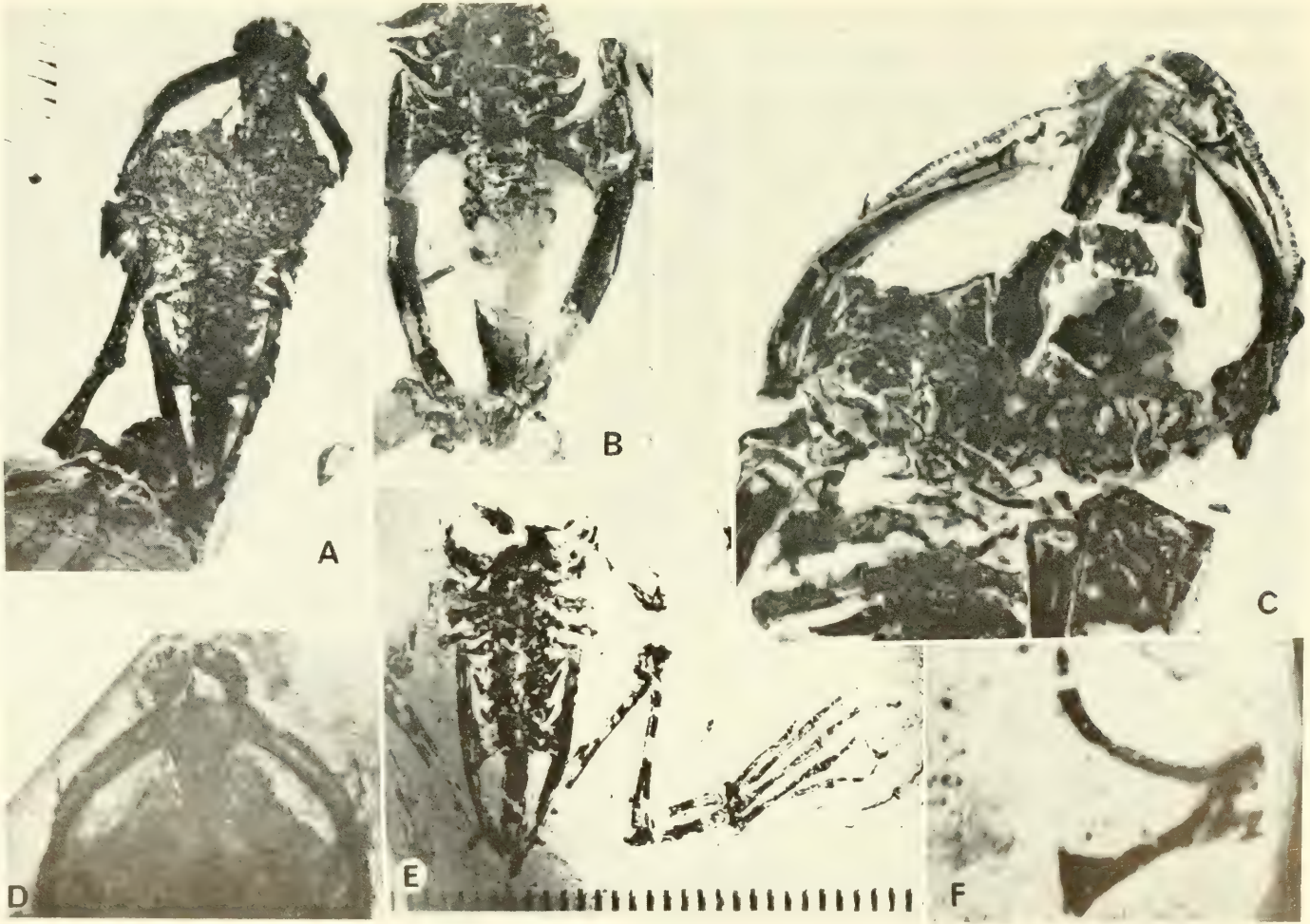

Plate 6. *Thoraciliacus rostriceps*, magnified × 3 unless otherwise specified. A. HUJZ, F 1 a; note rostrum, uncleft scapula, ribs, medioiliac articulation. The ilia contact the appendages of presacrals 4, 5, and 9. B. HUJZ, F 112; note three postsacrals. C. HUJZ, F 20, × 6; note teeth, parasphenoid, pectoral girdle. D. HUJZ, F 53; skull magnified × 6; note the rostrum consisting of the two nasals. E. HUJZ, F 41 a; note four ribs, medioiliac articulation, long pes. F. HUJZ, F 237; coracoid and clavicle, magnified × 6, in natural position.

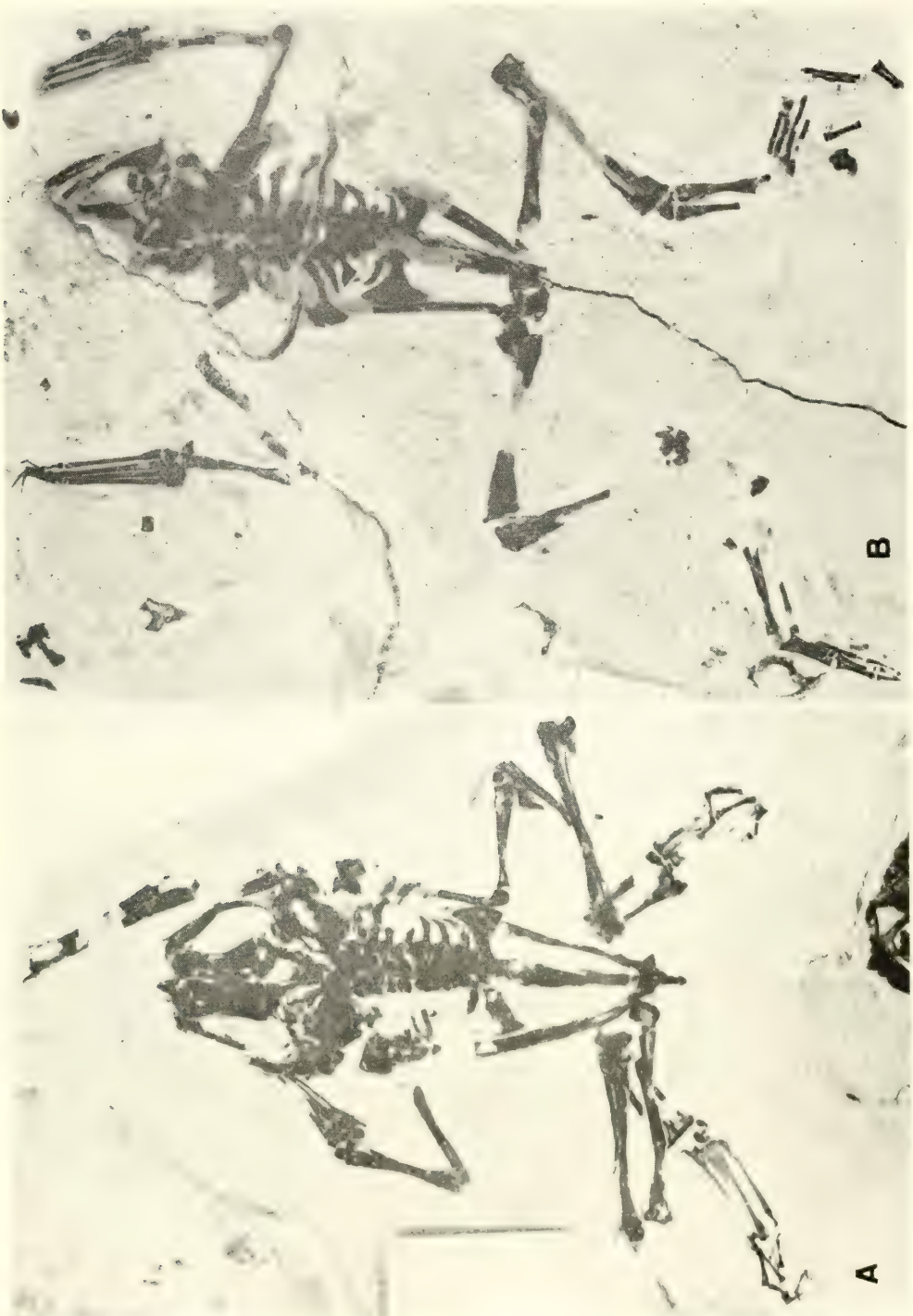

Plate 7. *Cordicephalus gracilis* n. gen., n. sp., early Cretaceous western Makhtesh Ramon, Israel; magnified × 3. A. Type specimen, HUJZ, F 165 a; compare drawing of Figure 6. B. HUJZ, F 168 a; note manus, pes, long ribs, and acroiliac articulation.

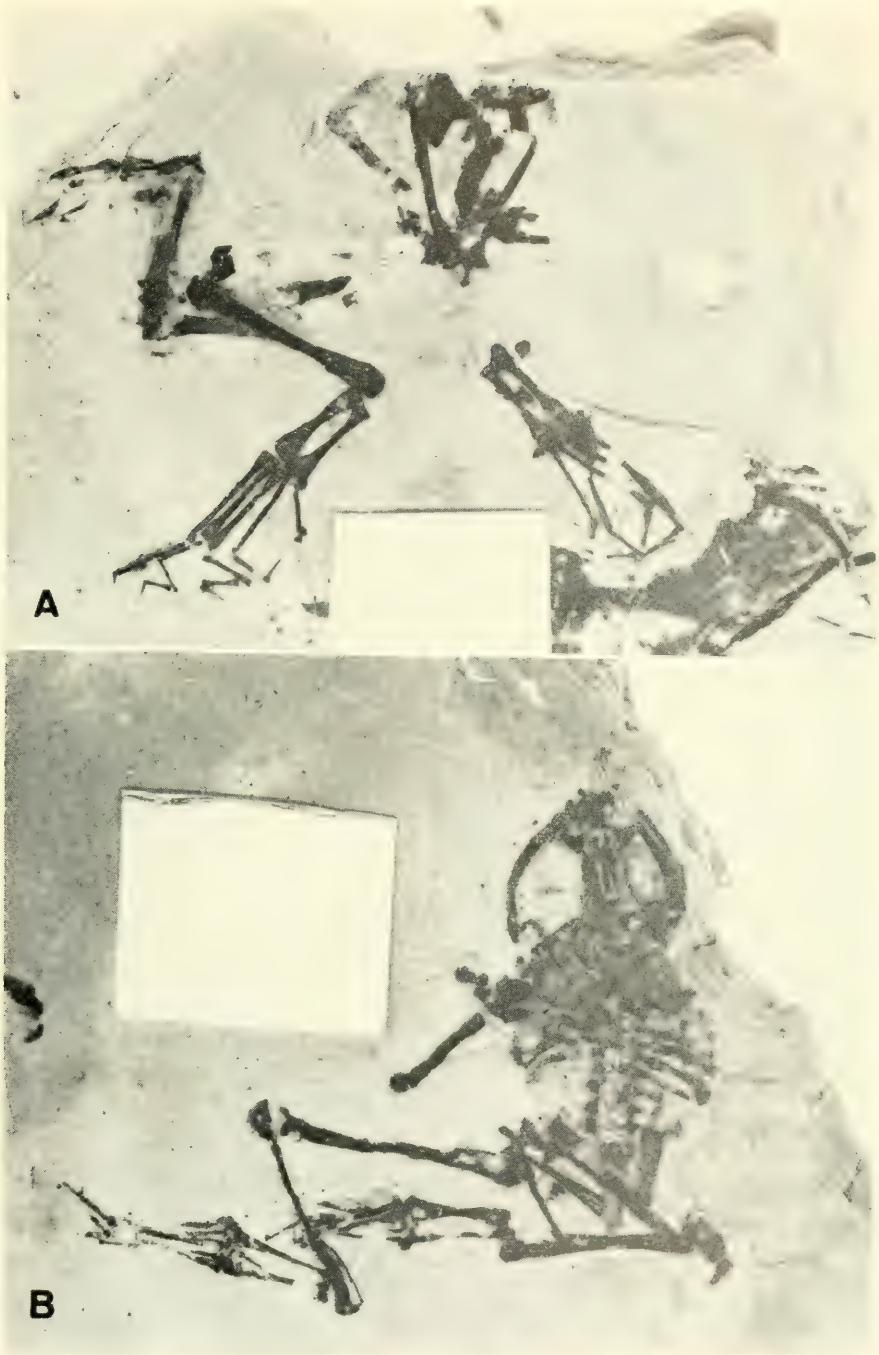

Plate 8. *Cordicephalus gracilis*, magnified × 3. A. HUJZ, F 177; note triangular pelvis, shape of sacral diapophysis, elongated pes with terminal pointed phalanges. B. HUJZ, F 197; note skull and four long ribs.

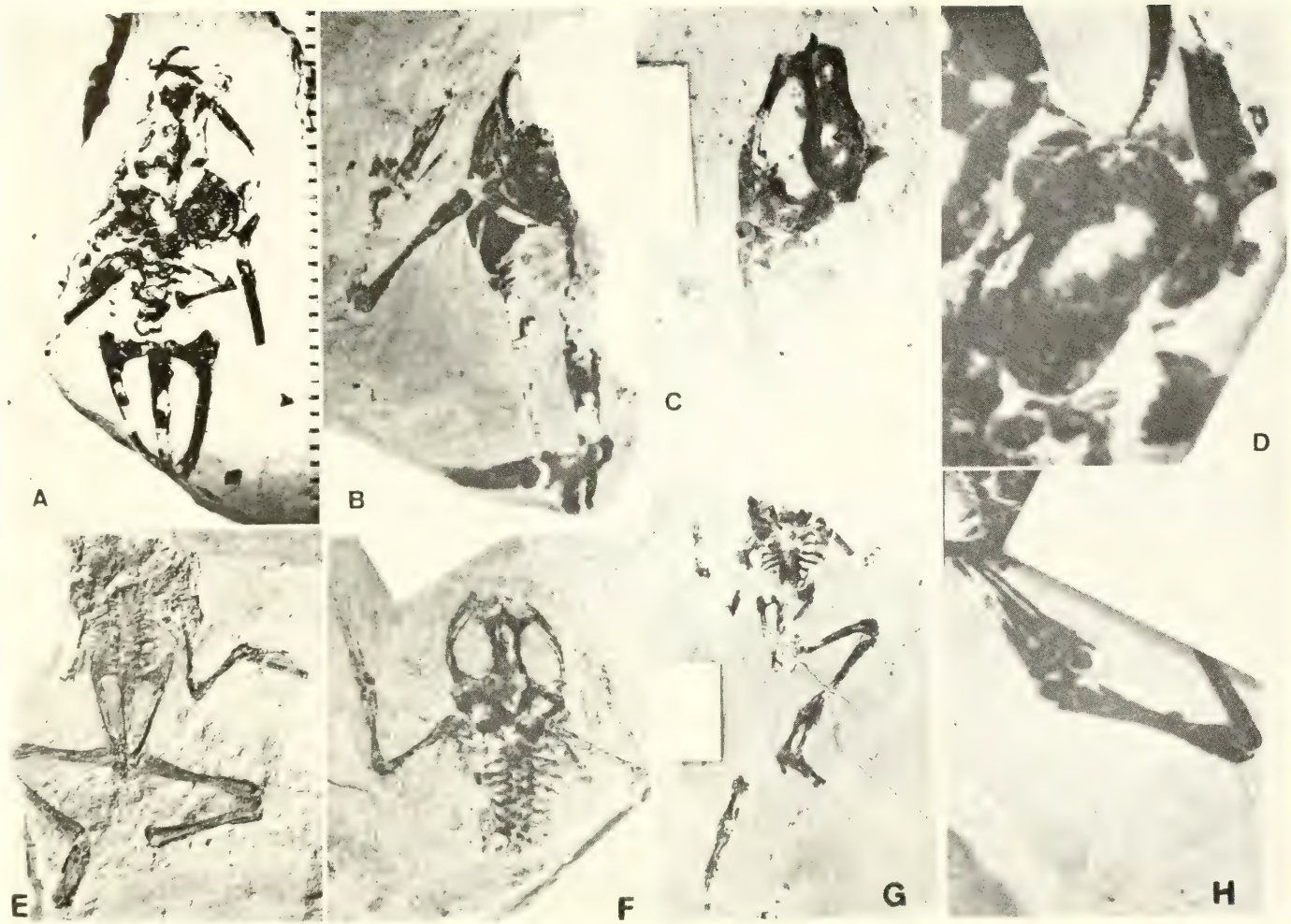

Plate 9. *Cordicephalus gracilis*, magnified × 3 unless otherwise specified. A. HUJZ, F 176 a; note coracoid and acroiliac articulation. B. HUJZ, F 201; note columella, coracoid, scapula, suprascapula and cleithrum. C. HUJZ, F 179 a; note shape of frontoparietals. D. HUJZ, F 165 a; note otic capsule, columella and operculum; × 9.5. E. HUJZ, F 151 b; × 2.2; note slenderness of the skeleton, long ribs, acroiliac articulation, triangular shape of pelvis. F. HUJZ, F 170 a; × 2; note skull and slenderness of skeleton. G. HUJZ, F 158; × 2; note ribs. H. HUJZ, F 165 a; × 6; note the shape and number of carpals; compare with Figure 6.

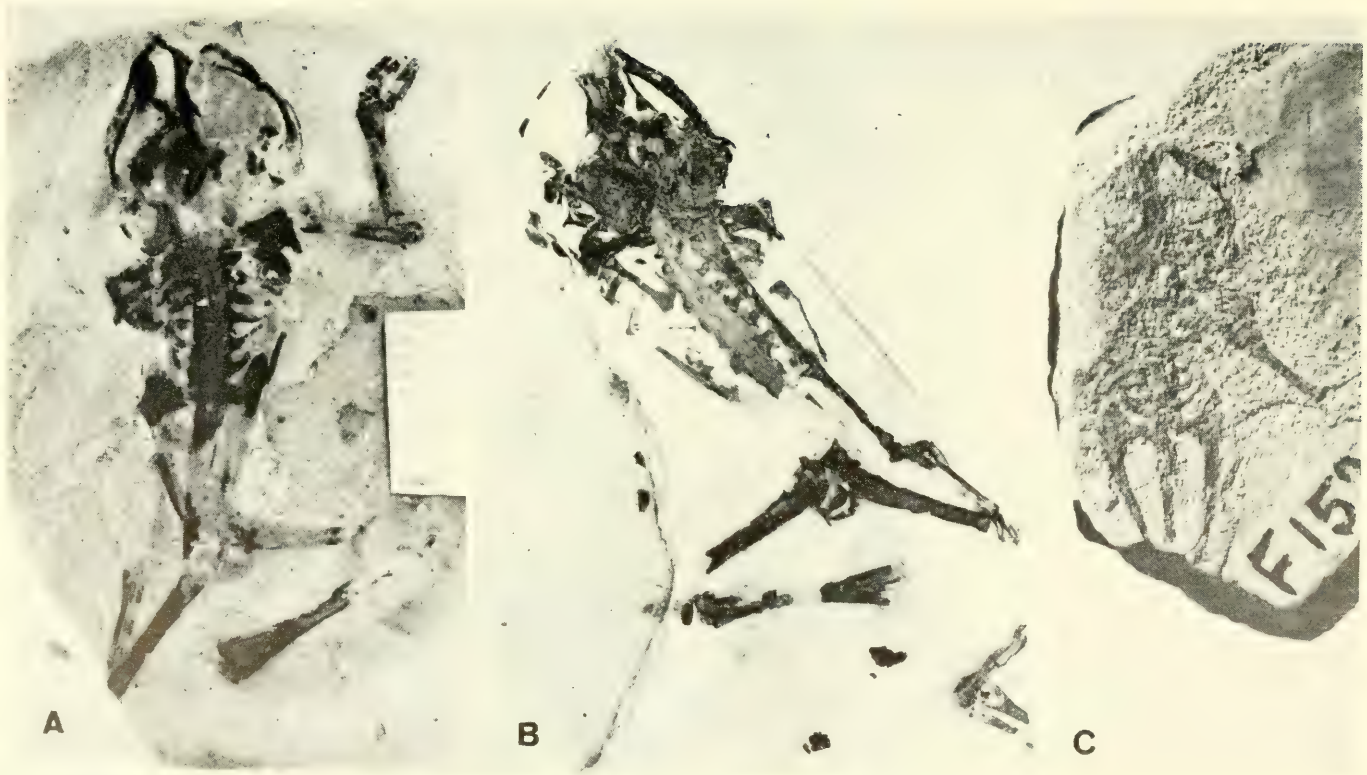

Plate 10. *Cordicephalus longicostatus* n. sp., early Cretaceous western Makhtesh Ramon, Israel. A. Type specimen, HUJZ F 171 a; compare with drawing on Figure 8. B. Counterpart of type specimen, HUJZ, F 171 b. C. HUJZ, F 152 a; note type of pelvis and the diapophyses of presacrals 6–8.

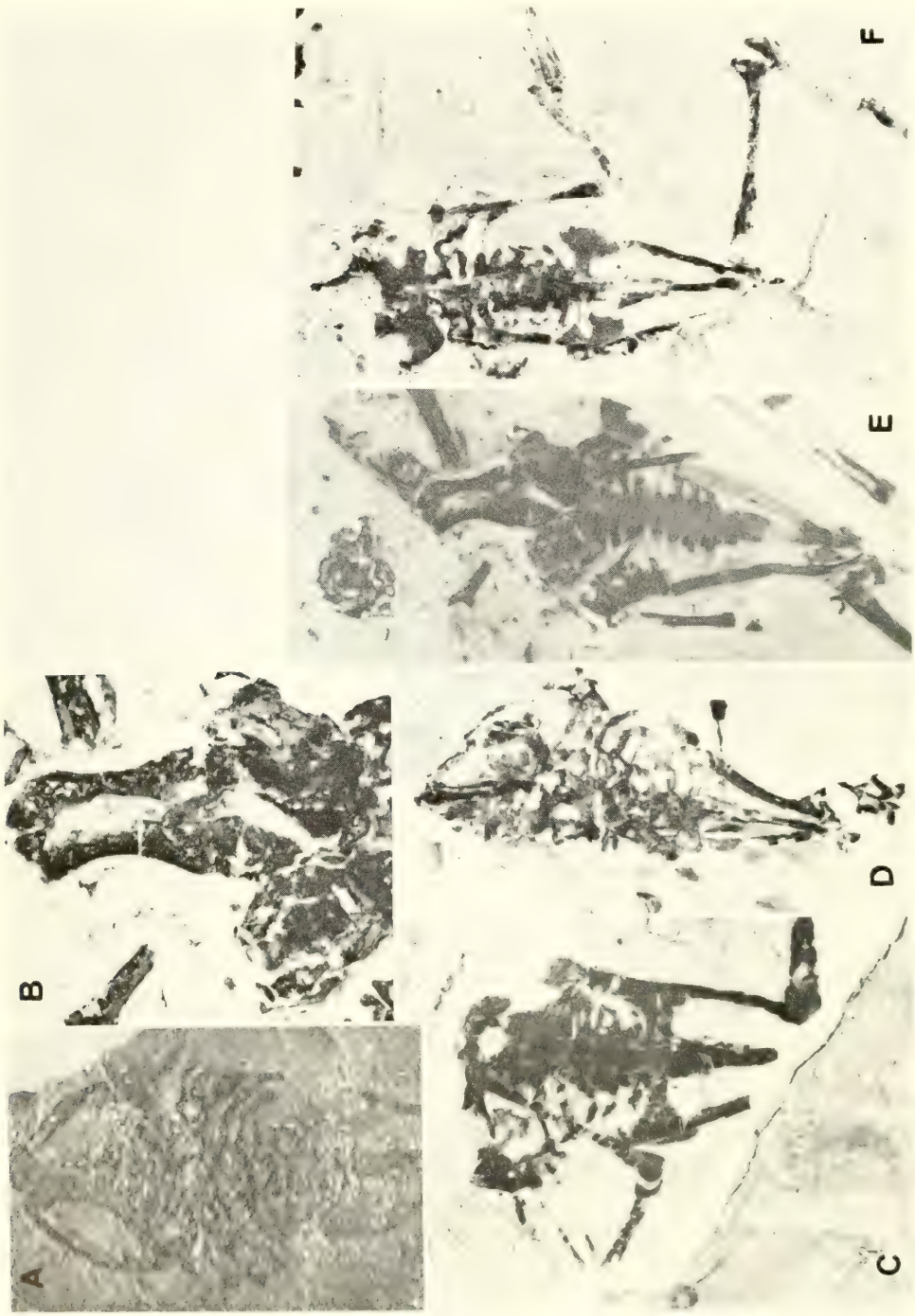

Plate 11. *Cordicephalus longicostatus*, magnified × 3. A. HUJZ, F 150 a; note four very long ribs. B. HUJZ, F 188; skull magnified × 6; note frontoparietals, subquadrangular shape of otic capsule, and bent columella on left side of the left otic capsule. C. HUJZ, F 185; note long humerus, capitate eminence, olecranon and elongated, manus. D. HUJZ, F 189 a; note long ribs and separated ischiopubic complex. E. HUJZ, F 188; note skull (enlarged on Fig. B on this plate), coracoid, and cleft scapula. F. HUJZ, F 156; note long ribs and long humerus, acroiliac articulation, and shape of pelvis.

Bulletin OF THE
Museum of
Comparative
Zoology

The Spider Genera *Gea* and *Argiope* in America (Araneae : Araneidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 9
APRIL 15, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
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Publications Office
Museum of Comparative Zoology
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THE SPIDER GENERA *GEA* AND *ARGIOPE* IN AMERICA (ARANEAE: ARANEIDAE)

HERBERT W. LEVI

This is the first publication in a series of revisions of North American orb weavers. Despite having studied representatives of the genera of the family Araneidae, I am not yet certain of the limits and diagnoses of the numerous araneid genera. The genus *Argiope* is an exception; the species belonging to it are readily placed. As the work progresses, I expect that the relative importance of the various characters will become increasingly apparent, and there will be less need to illustrate as lavishly as in this paper. As most North American species of *Argiope* have wide distributions into South America, I have found it advisable to include South American members of the genus. Even though *Argiope* includes our commonest spiders, the collections examined had many specimens erroneously determined, and the Central American and Mexican species have been confused. In this genus, as in other Araneidae, it is not at all easy to match males and females. The broken-off embolus tip of the male palp, found in the connecting ducts of the female, is often very useful in matching the sexes and identifying females of some difficult species (e.g. *Argiope argentata*, Figs. 130–133).

During the last 10 years the economic importance of spiders, particularly the orb weavers, has become recognized. Not only are they used as test animals for laboratory experimentation, but the value of spiders in natural control of insect pests is being studied. The difficulty in determining even common spiders is immense and has been a bottleneck in many researches. The few specialists with knowledge of spiders are overwhelmed with requests for determinations. Next to the Linyphiidae, the Araneidae are most difficult to determine at the present time, but fragmentation of the family into many meaningless genera, as in the Linyphiidae, luckily is less of a problem in the study of the Araneidae.

This research was supported in part by Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases. I am grateful to many colleagues for their help. Specimens were loaned by Dr. W. J. Gertsch of the American Museum of Natural History; Prof. M. Birabén and Dr. Olga Blanco of the Museum of the University of La Plata; Dr. L. Brundin of the Stockholm Natural History Museum; Dr. R. Crabill of the U. S. National Museum; Mr. J. Kekenbosch of the Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr. S. G. Lepneva of the Zoological Institute of the Academy of Sciences, Leningrad; Dr. M. Muma of the University of Florida; Dr. A. Riedel and W. Starega of Institute of Zoology, Polish Academy of Sciences; Prof. M. Vachon and Mr. J. F. Jézequèl of the Muséum National d'Histoire Naturelle, Paris; Prof. H. K. Wallace and Mr. K. J. Stone of the University of Florida; Dr. H. Weems of Florida State Museum, Gainesville; Dr. G. B. Wiggins of the Royal Ontario Museum, Toronto; Dr.

A. Willink and Mr. Z. Tomsic of the Instituto Miguel Lillo, Tucumán. Father Chrysanthus sent a gift of New Guinea species of *Argiope*; Dr. B. Y. Main sent specimens from western Australia; Dr. O. Kraus, Senckenbergische Naturforschende Gesellschaft supplied information; Dr. G. Owen Evans and Mr. D. L. Clarke of the British Museum (Natural History) checked types; Dr. C. Dondale checked specimens in the Canadian National collections; Mr. R. König supplied a photograph of *Argiope lobata*; and Mr. Robin Leech sent data on distributions in Canada.

The labels of the Wallace and Weems collections provided valuable ecological information from Michigan and Florida.

In this and all anticipated revisions, as in most of my theridiid revisions, I omit unillustrated literature records that lack voucher specimens in one of the large public spider collections. The reason for this is that I have found even the commonest species to be frequently misidentified in the literature.

ARANEIDAE Latreille, 1806

Araneides Latreille, 1806, Genera Crustaceorum et Insectorum, 1: 82. Family Araneides including the genus *Aranea* Linn. (= *Araneus* Clerck 1757), which is the type genus.

Araneidea Leach, 1817, Zoological Miscellany, 3: 47. Family Araneidea for species included in this family by Latreille.

Araneadae Leach, 1819, *in* Samouelle, Entomologists Useful Compendium. Family Araneadae including the genus *Aranea*, which is the type genus.

Epeirides Sundevall, 1833, Conspectus Arachnidum, p. 13. Type genus *Epeira* (= *Araneus*, objective synonym), subsequently used as Epeiridae.

Argiopidae Simon, 1890, Ann. Soc. Entomol. France, (6)10: 81. Type genus *Argiope*.

Araneidae Dahl, 1912, Handwörterbuch der Naturwissenschaften, 1: 502.

Note: Of the three family names, Epeiridae has been used most, Araneidae least. At the present time, Araneidae is used by German and some American authors, Argiopidae by the French (including Bonnet's catalog) and by many English and American authors. Epeiridae is no longer in use.

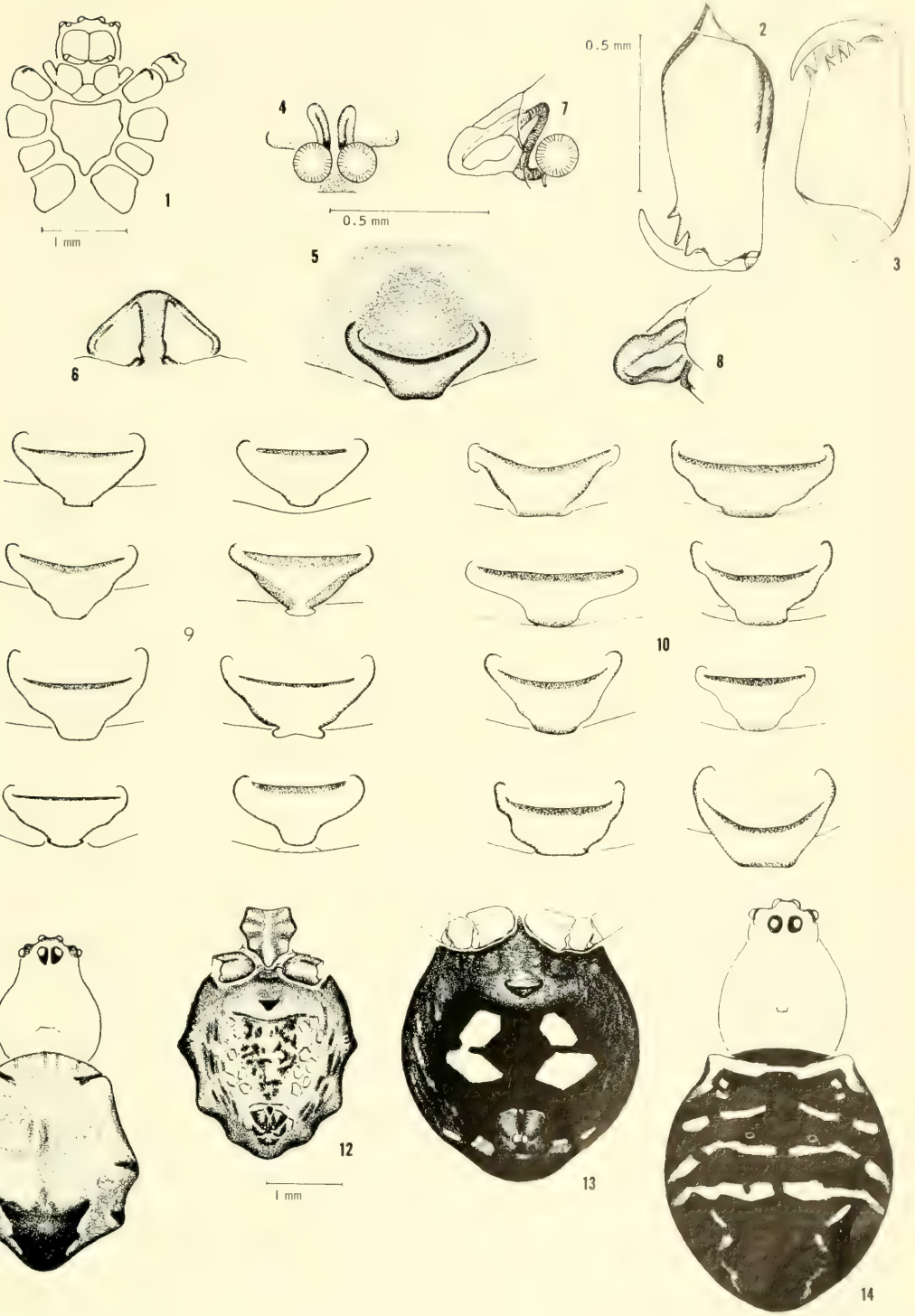
Bonnet, in his authoritative *Bibliographia Araneorum*, reasoned that the name Araneidae is so similar to the name of the Order Araneae as to create confusion; he therefore rejected Araneidae in favor of Argiopidae. However, if we were to follow Bonnet we would have to reject some of the commonest family names of animals, including Scorpionidae and Acaridae among the arachnids. To end the confusion resulting from use of three names for one family, I have applied The International Code of Zoological Nomenclature on the availability of family group names. The earliest emendation of Araneides to the current spelling, Araneidae, appears to be that of Dahl (Kaston, 1938, Amer. Midland Natur., 19: 640). An application to the International Commission on Zoological Nomenclature has been prepared requesting placement of the Araneidae Latreille, 1806 on the Official List of Family Names in Zoology.

Description. Araneidae are web spiders. They lack a cribellum and calamistrum, have no trichobothria on femora or tarsi, and have three claws on their tarsi. The legs are relatively short, covered with macrosetae ("spines")[1], but there is no comb on the fourth metatarsus. The eyes are arranged in two rows and in three groups, the median group of four eyes forming a square or trapezoid separated by

[1] A spine is defined in American dictionaries as a "stiff, pointed external process" (Pennak, 1964, Collegiate Dictionary of Zoology, Ronald Press).

→

Gea heptagon (Hentz) female. Fig. 1. Ventral view of sternum and coxae. Figs. 2, 3. Left chelicera. 2. Anterior view. 3. Posterior view. Figs. 4–8. Epigynum. 4. Dorsal view. 5. Ventral view. 6. Posterior view. 7, 8. Lateral view. Fig. 9. Epigyna of eight individuals from Cameron, Louisiana. Fig. 10. Epigyna of eight individuals from Washington Co., Arkansas. Fig. 11. Dorsal view, Louisiana. Fig. 12. Ventral view of abdomen, Louisiana. Fig. 13. Ventral view of abdomen, St. Croix, West Indies. Fig. 14. Dorsal view, St. Croix, West Indies.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some distance from the two lateral eyes on each side. The eyes are all alike. The area between the eyes and the border of the carapace, the so-called "clypeus" (better called front), is low, less than the height of the eye region. Anatomically, the clypeus is the area behind the chelicerae, and the name might better be abandoned in taxonomic discussions.

The chelicerae may lack the anterior dorsal projection under the front that is present in many Theridiidae and that serves for muscle attachment. This projection may be present in the Argiopinae. On the face of the chelicerae below the front may be a knob, little developed in Argiopinae. The chelicerae are strong with two rows of teeth and a short, strong fang. The labium has the anterior edge swollen or "rebordered." There are six spinnerets (Fig. 66).

The paracymbium (P in Figs. 19, 20) of the male palpus is attached to the proximal end of the cymbium; it is not a free sclerite as in the Linyphiidae.

Most of the Araneidae construct orb webs; the spider hangs in the web head down.

At present I do not know the limits of family, nor can I judge whether Tetragnathinae belong to the family. The inclusion of *Tetragnatha* has no bearing on the family name, according to the International Code of Zoological Nomenclature (1961), as the family name is attached to the genus *Araneus* no matter what else is included in the family.

Subfamily ARGIOPINAE Simon 1890

Argiopidae Simon, 1890, Ann. Soc. Entomol. France, (6)10: 81. Type genus *Argiope*.

Argiopinae Simon, 1895, Histoire Naturelle des Araignées, 1: 759.

The posterior eye row, seen from above, is strongly procurved (Figs. 14, 43, 58). The anterior lateral eyes are smaller than the other eyes (Figs. 17, 74, 102, 127). The anterior boss on the chelicerae (Figs. 2, 3, 46–48, 63–64) is relatively small, and the anterior face has a proximal pointed apodeme similar to that of theridiids (Figs. 2, 3, 46, 47).

Of the first pair of legs, the coxae and trochanters each have a ventral tubercle or ridge (Figs. 1, 92, 114–115, 139). The tarsus and metatarsus combined is longer than the patella and tibia of each leg. The labium is wider than long (Fig. 65). Males are much smaller than females.

The male palpi (Figs. 19–20, 39, 42) resemble those of theridiids. The terminal apophysis characteristic of *Araneus* is lacking, and the tip of the embolus breaks off when mating and remains in the female tubes probably in all species of *Argiope*.

The spiders hang in the center of the almost vertical orb web and do not have a retreat (Plate I, fig. 2; Plate II).

Three genera were included in the subfamily: *Argiope*, *Gea* and *Mecynogea*. *Mecynogea* does not belong to the subfamily.

MECYNOGEA Simon 1903

Hentzia McCook, 1894, American Spiders, 3: 244. Type species by monotypy *Epeira basilica* McCook. Name preoccupied by *Hentzia* Marx, 1883, in Howard's List of Invertebrate Fauna of South Carolina, p. 26.

Mecynogea Simon, 1903, Ann. Soc. Entomol. Belgique, 47: 25. Type species by subsequent designation (Petrunkevitch, 1928, Trans. Connecticut Acad. Sci. 29: 135) *M. bigibba* Simon 1903, from Brazil, examined.

Allepeira Banks, 1932, Publ. Oklahoma Biol. Surv. 4: 23. New name to replace *Hentzia* McCook. NEW SYNONYMY.

Key to Genera of Argiopinae

1a. Anterior median eyes equally spaced or closer to laterals (Figs. 1, 17); adult females smaller than 6 mm 2

1b. Anterior median eyes usually closer to each other than laterals (Figs. 44, 59, 94); adult females larger than 9 mm ..... *Argiope*

2a. Adult females ..... *Gea*

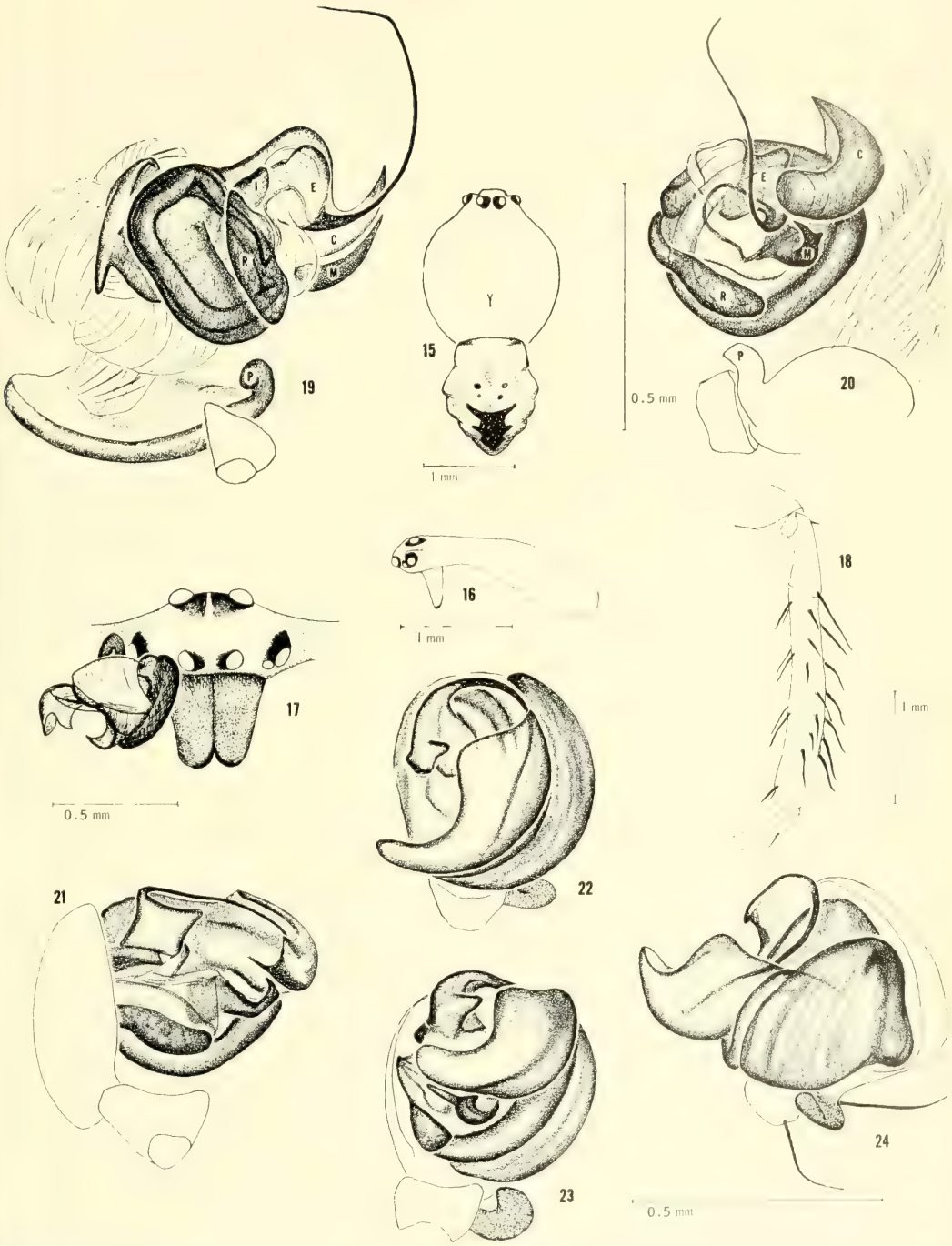
2b. Adult males 3a

3a. First tibia curved and bearing strong macrosetae (Fig. 18). ..... *Gea*

3b. First tibia straight and armed as other legs are (Fig. 73) ..... *Argiope*

GEA C. L. Koch 1843

Gea C. L. Koch, 1843, Die Arachniden, 10: 101. Type species by monotypy *Gea spinipes* C. L.



Gea heptagon (Hentz), male. Fig. 15. Dorsal view. Fig. 16. Lateral view of carapace and chelicerae. Fig. 17. Eyes and chelicerae. Fig. 18. First left patella and tibia, prolateral view. Figs. 19–24. Left palpus. 19–20. Expanded. 21. Mesal view. 22, 23. Ventral view. 24. Ectal view.

Abbreviations: C, conductor; E, embolus; I, stipes; M, median apophysis; P, paracymbium; R, radix.

Koch, *ibid.*, 10: 101, pl. 823, from the East Indies.

Koch could not determine the sex of the specimen he described, as the palpi were missing and the abdomen shrivelled. The specimen, belonging to the Berlin Museum, could not be located in 1966.

Despite the incomplete description, it has been assumed, since the time of Simon, that *Gea* differs from *Argiope* in having the anterior eyes evenly spaced. This is not apparent in the Koch illustration. Furthermore, young *Argiope*, and often small males, also have the anterior eyes evenly spaced. The species *Gea heptagon* has always been associated with *Gea*, and it is best to keep it in the genus until more knowledge about the characters of the different genera of Araneidae becomes available.

Another character that separates the genera is the modified first tibia, curved and armed with macrosetae in males of *Gea* (Fig. 18), unlike that of *Argiope* (Fig. 73). Koch's specimen may have been a male, as the first tibiae appear to be curved and armed in the illustration.

According to Simon (1895, Histoire Naturelle des Araignées, 1: 768), *Gea* does not make a stabilimentum.

Of the numerous species described from the Americas, some are *Gea heptagon*, others juvenile *Argiope*. Many were described by Franganillo, whose descriptions of Cuban spiders are barely recognizable, and who did not make holotypes. His collection is kept at the Institute of Zoology, Academia de Ciencias de Cuba, La Habana. The collection, though well preserved has no labels, only numbers glued to bottles. No catalog is known to exist (personal communication Dr. P. Alayo D., March, 1967.)

The *Gea* species described from America with their probable synonymy are:

Gea bimucronata Mello-Leitão, 1936, Rev. Chilena Hist. Natur., 40: 125, fig. 14. Female, probably mature, possibly *Argiope trifasciata*. The holotype is probably in the Rio Museum but could not be examined.

Gea decorata Thorell var. *varians* Franganillo, 1926, Bol. Soc. Entomol. España, 9: 12, Cuba. The coloration suggests a juvenile *Argiope argentata*.

Gea integra Franganillo, 1930, Invest. Inst. Nac. Cienc. Havana, 1: 19, Cuba. The sketch of the narrow abdomen with a tubercle on each side suggests a juvenile *Gea heptagon*. Scattered pigment was probably mistaken for the epigynum.

Gea lineata Franganillo, 1926, Bol. Soc. Entomol. España, 9: 53, Cuba. Coloration and lack of tubercles suggest a juvenile *Argiope trifasciata*.

Gea panamensis Chamberlin, 1916, Bull. Mus. Comp. Zool., 40: 243, pl. 19, fig. 8, ♂. Male holotype from Panama, in the Museum of Comparative Zoology, examined, is *Argiope argentata*.

Gea partita Franganillo, 1930, Invest. Inst. Nac. Ciencia, 1: 17, Cuba. This may be a juvenile *Gea heptagon*, and the description of the epigynum that of scattered pigment spots.

Gea praedicta O. P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, 1: 267, pl. 37, fig. 11 ♂. Male holotype from Teapa, Tabasco, Mexico, in the British Museum, is *Gea heptagon*.

Gea severinoi Mello-Leitão, 1917, Broteria, 15: 91. Female from Bello Horizonto, Minas Gerais. This species makes a stabilimentum and the description indicates that it is a juvenile *Argiope argentata*. The holotype was not available for examination.

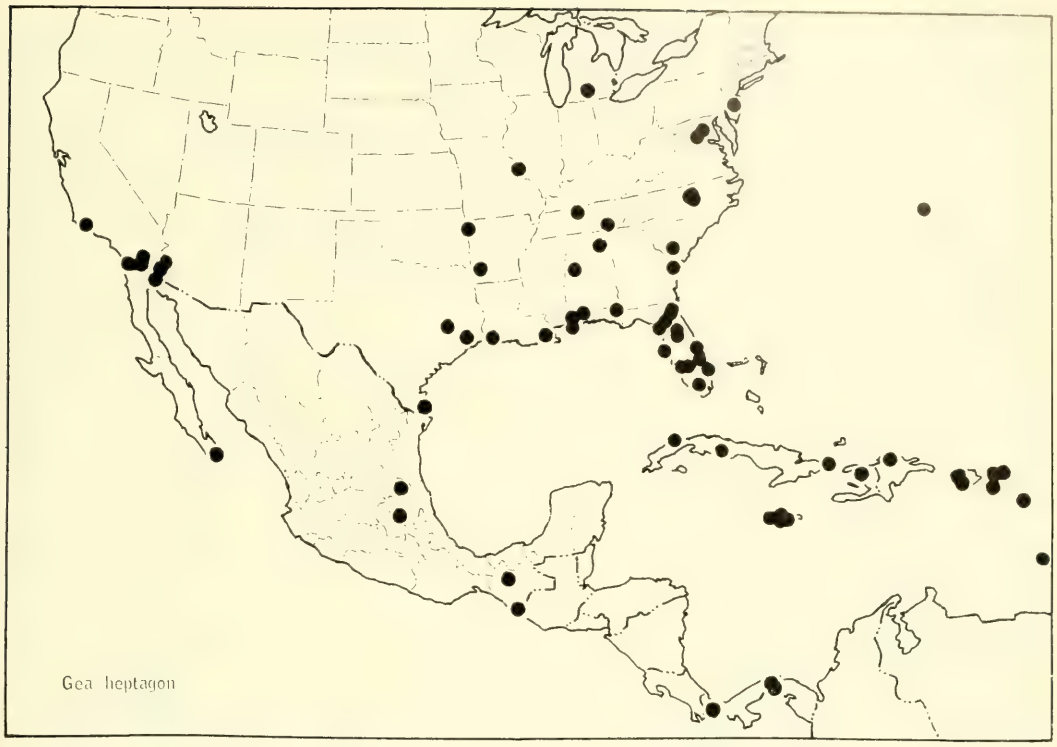
Gea subarmata Thorell var. *maculata* Franganillo, 1930, Invest. Inst. Nac. Ciencia, 1: 19, Cuba. The description appears to be that of a *Gea heptagon*.

Gea heptagon (Hentz)

Figures 1–24; Map 1

Epeira heptagon Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 20. Type localities, North Carolina and Alabama; specimens lost.

Gea heptagon,—Keyserling, 1892, Die Spinnen Amerikas, 4: 76, pl. 3, fig. 58, ♀. McCook,



Map 1. Distribution of *Gea heptagon* (Hentz).

1893, American Spiders, 3: 208, pl. 12, fig. 8, ♀. Tullgren, 1901, Bihang Svensk. Vet. Akad., 27: 9, fig. 5, ♂. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 243, figs. 93–96, ♀♂. Roewer, 1942, Katalog der Araneae, 1: 746. Bonnet, 1957, Bibliographia Araneorum, 2: 1982.

Gea praedicta O. P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, 1: 267, pl. 37, fig. 11, ♂. Male holotype from Teapa, Tabasco, Mexico, in the British Museum (Natural History), examined by D. Clark and compared to my figures. NEW SYNONYMY.

Gea heptagon var. *nigra* Petrunkevitch, 1930, Trans. Connecticut Acad. Sci. 30: 245, figs. 97–100. Female holotype from Puerto Rico, lost. NEW SYNONYMY.

? *Gea integra* Franganillo, 1930, Invest. Inst. Nac. Cienc. Havana, 1: 19, Cuba. NEW SYNONYMY.

? *Gea partita* Franganillo, 1930, *ibid.* 1: 17, Cuba. NEW SYNONYMY.

? *Gea subarmata* Thorell var. *maculata* Franganillo, 1930, *ibid.*, 1: 19, Cuba. NEW SYNONYMY.

Gea ergaster,—Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8 (5): 104. Not *Epeira ergaster* Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 55.

Note: Franganillo's names have insufficient descriptions to place them with certainty. The Chamberlin and Ivie (1944) synonymy of *Gea heptagon* with the older *Epeira ergaster* is an error. Walckenaer's name has Abbot manuscript figure 235 as holotype. Abbot's figure shows a light brown spider, probably of the genus *Araneus*, certainly not *Gea heptagon*. (Color photographs of Abbot illustrations and a microfilm are in the Museum of Comparative Zoology.) The Abbot specimens, found in a wasp nest, were presumably illustrated when dry. There is no need to change the widely accepted name of this species.

Description. Male. Carapace yellow-

brown, legs yellow-brown. Abdomen shield-shaped with lobes on sides, a black patch on posterior part. Anterior median eyes largest; anterior lateral eyes smallest, one-half size of posterior laterals. Anterior median eyes one diameter apart, one diameter from laterals. Posterior median eyes two diameters apart, more than two diameters from laterals. Posterior median eyes three diameters from anterior medians. Total length 2.6 mm. Carapace 1.7 mm long, 1.5 mm wide. First femur, 2.1 mm; patella and tibia, 2.2 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm. Second patella-tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Female. Carapace yellow-brown. Sternum with longitudinal median light line and white lines going laterally to the coxae. Legs yellow-brown with dark bands. Dorsum of abdomen white with a median posterior dark triangle (Fig. 11). Venter with white pigment spots and median line of dark spots (Fig. 12). Anterior median eyes one and one-half diameters apart, one and one-half diameters from laterals. Posterior median eyes one and one-quarter diameters apart, two and one-half diameters from laterals. Total length 4.5 mm. Carapace 1.9 mm long, 1.8 mm wide. First femur, 2.3 mm; patella and tibia, 2.5 mm; metatarsus, 1.9 mm; tarsus, 0.5 mm. Second patella and tibia, 2.1 mm; third, 1.3 mm; fourth, 2.1 mm.

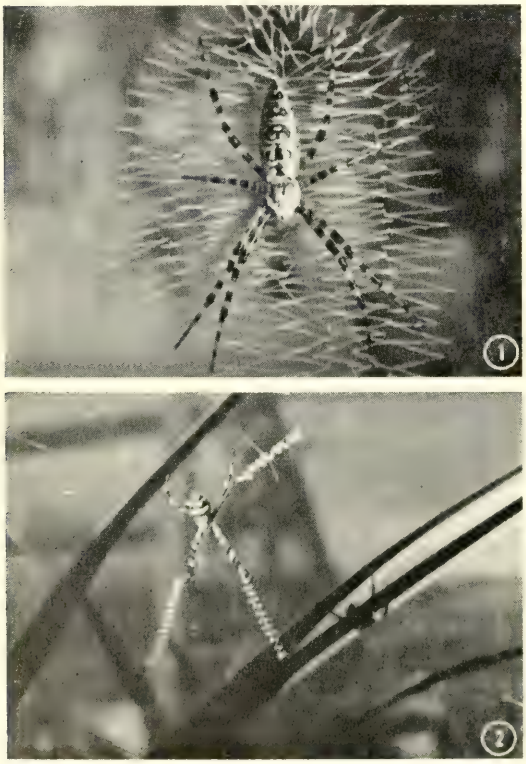


Plate I. Fig. 1. Juvenile *Argiope trifasciata* hanging in web; from Liberty Co., Florida. (Photo by H. K. Wallace.) Fig. 2. Adult *Argiope argentata* hanging in web; from Plantation Key, Florida.

Specimens from the West Indies have light, probably silver, transverse bands, more contrasting (Fig. 14) than in specimens from the southeastern United States. The specimens with most contrast came from Puerto Rico and the West Indies (Figs. 13, 14). McCook (1893) indicated and illustrated some of the light areas of the abdomen as metallic silver similar to the color of many species of *Argiope*. Petrunkevich (1930) described the light areas as pearly white.

Habits. Despite the common occurrence of *Gea heptagon*, there are no adequate descriptions of its habits or of its web. The web appears to lack a stabilimentum and the viscid spiral is dense. The web is perpendicular and on the slightest disturbance the spider will drop out of it (Hentz, 1850). The web is probably made in low herbaceous vegetation (J. Beatty, pers. comm.). In large collections obtained by A. M. Chickering in the West Indies in 1966, *Gea heptagon* was common, but was never collected with *Argiope trifasciata*. Both species were collected with *Argiope argentata*.

Distribution. Michigan, New Jersey to West Indies, west to southern California, south to Panama.

Records. Several collections are available from the vicinity of Albion, Michigan; there is a literature record from southern Wisconsin. The species is common in the West Indies as far south as St. Lucia (Map 1).

Plate II. Web of *Argiope florida* Chamberlin and Ivie, showing the four stabilimenta. The spider hangs head down in the hub on the right side of web. (Photo by Dr. T. Eisner, courtesy of Amer. Assoc. Adv. Sci. and T. Eisner.)

ARGIOPE Audouin 1826

Argyope Audouin, 1826, Explication sommaires des planches d'Arachnides de l'Egypte et de la Syrie *in* Savigny's Descriptions de l'Egypte et de la Syrie (4): 121. Type species designated by Thorell, 1869, On European Spiders, p. 51, *Argiope lobata* (= *A. sericea* Olivier,—Audouin, 1826).

Argiope,—Audouin, 1827, *ibid.*, 2 ed., 22: 328. Thorell, 1869, On European Spiders, p. 51. Emendation of generic name used by almost all later authors. Bonnet, 1955, Bibliographia Araneorum, 2: 667.

Argyopes,—Latreille, 1829, Les Arachnides, *in* Cuvier, La Règne Animale, p. 548. (This form was used by several authors before 1875.)

Miranda C. L. Koch, 1835 in Herrich—Schaeffer, Deutschlands Insekten, Heft 128, pl. 14. Type species *Miranda transalpina* C. L. Koch [= *Argiope bruennichi* (Scopoli)]. *Miranda* was first synonymized with *Argiope* by Thorell, 1869, On European Spiders, p. 51.

Argiopes,—L. Agassiz, 1846, Nomenclator Zoologicus, Soloduri, Arachnidae, p. 2.

Metargyope F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 451. Type species by monotypy *A. trifasciata*.

Notes: 1. The word *Argiope* is derived from the Greek for brilliant eye [Αργίοπη] and would today require an i in its spelling (Appendix B, Internat. Code Zool. Nomencl.). In no place is the name spelled with an i in the first edition. In the second edition, *Argiope* appears with i. Thorell, 1869 (the first of several authors to do so), considered *Argiope* to be an emendation by the original author.

2. The name of the genus has been spelled for almost 100 years with an i. It has never been spelled with y in the American literature or in the combination *Argiope aurantia*. In the combination *A. trifasciata*, the common cosmopolitan species, the genus has been spelled with y by only four authors in five publications, while 53 authors in over 100 publications spelled it with i up to 1938 (Bonnet, 1955).

3. Bristowe, in his book *Comity of Spiders* (1939, Ray Soc., London), spelled the family name with y. Judging by other changes made, Bristowe was unaware of the importance of keeping the spellings of scientific names unchanged and also of the provisions of the International Code on Zoological Nomenclature (for seeking relief from unnecessary changes brought about by strict adherence to the Code). Roewer's *Katalog der Araneae* (1952–1954), while a very useful compendium, changed numerous spellings from long accustomed usage. The authoritative *Bibliographia Araneorum* of Bonnet (1945–1961) avoided such changes by discussing in footnotes any problems concerning the correct spellings in use since the time of Thorell.

4. Unfortunately, some German authors, particularly W. Crome, have followed Roewer, apparently unaware of possible errors and of the discussion in Bonnet's catalog. Crome, in his studies on the biology of *Argiope bruennichi*, used the spelling with y. The only recent taxonomic work on *Argiope* is that of Father Chrysanthus (1958, 1961), on New Guinea spiders, who was advised to use the spelling with y.

5. There appear to be two general interpretations of the Code on Zoological Nomenclature. One favors strict adherence to the Code, relief from its strictures to be sought by application of the individual case to the International Commission of Zoological Nomenclature, and considers that the 50-year statute of limitations requires such a procedure. No issue can be taken with this view except the enormous amount of

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Argiope lobata (Pallas). Figs. 25–35. Epigynum. 25. Dorsal view, USSR. 26. Ventral view, USSR. 27. Posterior view, USSR. 28. Lateral view, USSR. 29. Dorsal view, Italy. 30. Ventral view, Italy. 31. Posterior view, Italy. 32. Lateral view, Italy. 33. Dorsal view, France. 34. Ventral view, France. 35. Posterior view, France. Fig. 36. Female. Fig. 37. Left palpus, mesal view (Isl. Tremiti, Italy). Fig. 38. Palpus, ectal view (Isl. Tremiti, Italy).

Argiope bruennichi (Scopoli). Figs. 39–41. Left palpus. 39. Expanded. 40. Mesal view. 41. Ectal view.

Argiope argentata (Fabricius). Fig. 42. Left palpus expanded.

Abbreviatons: C, conductor; E, embolus; I, stipes; M, median apophysis; R, radix.

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33
34
35
36
37
38
0.5 mm
E
C
M
R
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40
41
0.5 mm
42
0.5 mm

non-constructive and time-consuming work in making the applications, and the disagreements that arise over small details in applications.

The other view is that names should be freely changed about in strict accord with the text of the Code. The proponents feel that only in this way will final stability come about. This is not a convincing argument considering that one still finds the name *Miranda* (a synonym of *Argiope*) in catalogs of biological supply houses and in popular literature, and the name Attidae in the technical literature although Attidae was supplanted by Salticidae at the turn of the century, when the name *Attus* (Walckenaer 1805) was found to be a synonym of *Salticus* Latreille 1804 (Bonnet, 1955, *Bibliographia Araneorum*, 2: 781). Also the junior objective synonyms of *Araneus*, *Aranea* and *Epeira* continue to be used.

The spellings in Roewer's Katalog have unfortunately only added to our nomenclatural burden and have added unnecessary synonyms where there has been relative stability since the time of Thorell. Each case has to be considered individually. Roewer, unlike Bonnet, did not discuss the problems of name spellings. Therefore, when in doubt, we may have to consider the possibility that mistakes were made by Roewer.

The interpretation of the Code shared by a number of North American spider specialists familiar with the Code (consulted in letters during summer 1966) is that the spelling of the generic names used in Bonnet's authoritative *Bibliographia Araneorum* should be continued and that the continuity and stability of scientific animal names is paramount.

It should also be pointed out that in regard to original spellings the recent (1961) International Code of Zoological Nomenclature has a change from the previous (French) version, which condoned later emendation. No provision, except through the Statute of Limitations, was made in the new (1961) Code to bring relief in the very many cases in the Animal Kingdom in which the emended spelling has become the accepted name.

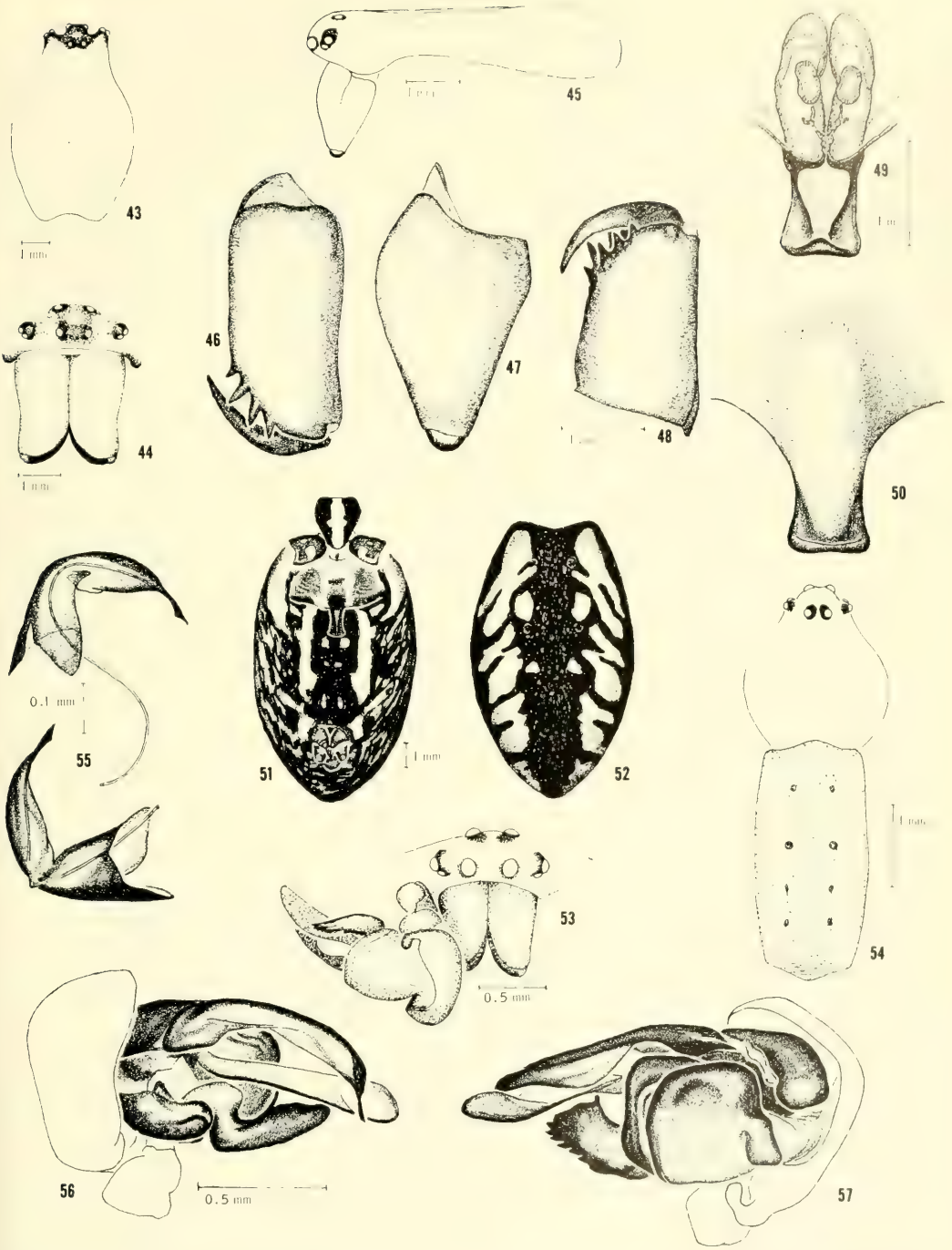
6. A formal application to the International Commission on Zoological Nomenclature to preserve the name *Argiope* has been made.

7. An added complication is the homonym *Argiope* Eudes-Deslongchamps 1842, for a brachiopod, the name of which was promptly emended to *Argyope* Davidson, 1850 (according to Neave 1939, *Nomenclator Zoologicus*, 1: 293). This name has been replaced by *Megathiris* d'Orbigny, 1847 (see Schuchert, 1929, *Fossilium Catalogus*, part 42, Brachiopoda), according to information kindly supplied by Dr. G. A. Cooper of the United States National Museum, presumably because *Argiope* Eudes-Deslongchamps was considered a junior homonym of *Argiope* Audouin. The use of the name *Argyope* in spiders may thus affect the stability of names of brachiopods.

Diagnosis. Argiope differs from other araneids (except *Gea*) in having the posterior eye row strongly procurved (Fig. 36). The anterior lateral eyes are smaller than the posterior laterals (Figs. 45, 74, 102). Each of the posterior median and lateral eyes has a boat-shaped tapetum in the lateral half, a grate-shaped tapetum in the median half. The boss on the anterior face of chelicerae is relatively small (Figs. 46–48) and the chelicerae are much weaker than in *Araneus*, and are sometimes inclined posteriorly at the distal end.

The leg metatarsus and tarsus is longer than the patella and tibia. The abdomen of females is shield-shaped (Figs. 36, 52, 61), that of males and juveniles longer than wide (Figs. 54, 76, 103, 128, 148).

All make a nearly vertical orb web having a stabilimentum or two stabilimenta crossing (in *A. argentata* and *A. florida* Plate I; Plate II). The stabilimentum is always more elaborate in young than in adults (Plate I). Despite its name, the white bands do not function in support of the



Argiope aurantia Lucas. Figs. 43–45. Female carapace and chelicerae. 43. Dorsal. 44. Anterior 45. Lateral. Figs. 46–48. Left female chelicera. 46. Anterio-mesal. 47. Lateral. 48. Ventral. Figs. 49–50. Epigynum. 49. Dorsal view. 50. Ventral view. Figs. 51–52. Female abdomen. 51. Ventral. 52. Dorsal. Fig. 53. Male eyes, chelicerae and palpus. Fig. 54. Male, dorsal view. Fig. 55. Tips of a male embolus retrieved from female epigynum. Fig. 56–57. Left palpus. 56. Mesal. 57. Ectal.

web; webs of the largest females often lack a stabilimentum. It may obscure the outline of the spider, which does not have a retreat but hangs in the center of the web (Plate II). However, there is no experimental evidence for this theory. The stabilimentum may help guide males to the female (Crome and Crome, 1961b). The frame of the web may extend on each side of the orb and may be strengthened by the spider. It is not periodically replaced, as is the viscid silk.

The genus *Gea* has been separated because the eyes of the anterior row are evenly spaced or closer to laterals. Often they are so in *Argiope*, and as this is an allometric growth character, it does not hold to separate juvenile specimens of the genera. Small *Argiope* and males (Figs. 53, 102, 162) have the same arrangement as does *Gea*. Adult *Argiope* generally have the anterior median eyes closer to each other than to the laterals, but they are only slightly closer in some species. The males of *Gea* have the first tibia curved and with strong, large setae (Fig. 18); those of *Argiope* are not modified (Fig. 73).

Color illustrations of the commonest species will be published in a forthcoming book (Levi and Levi, in press).

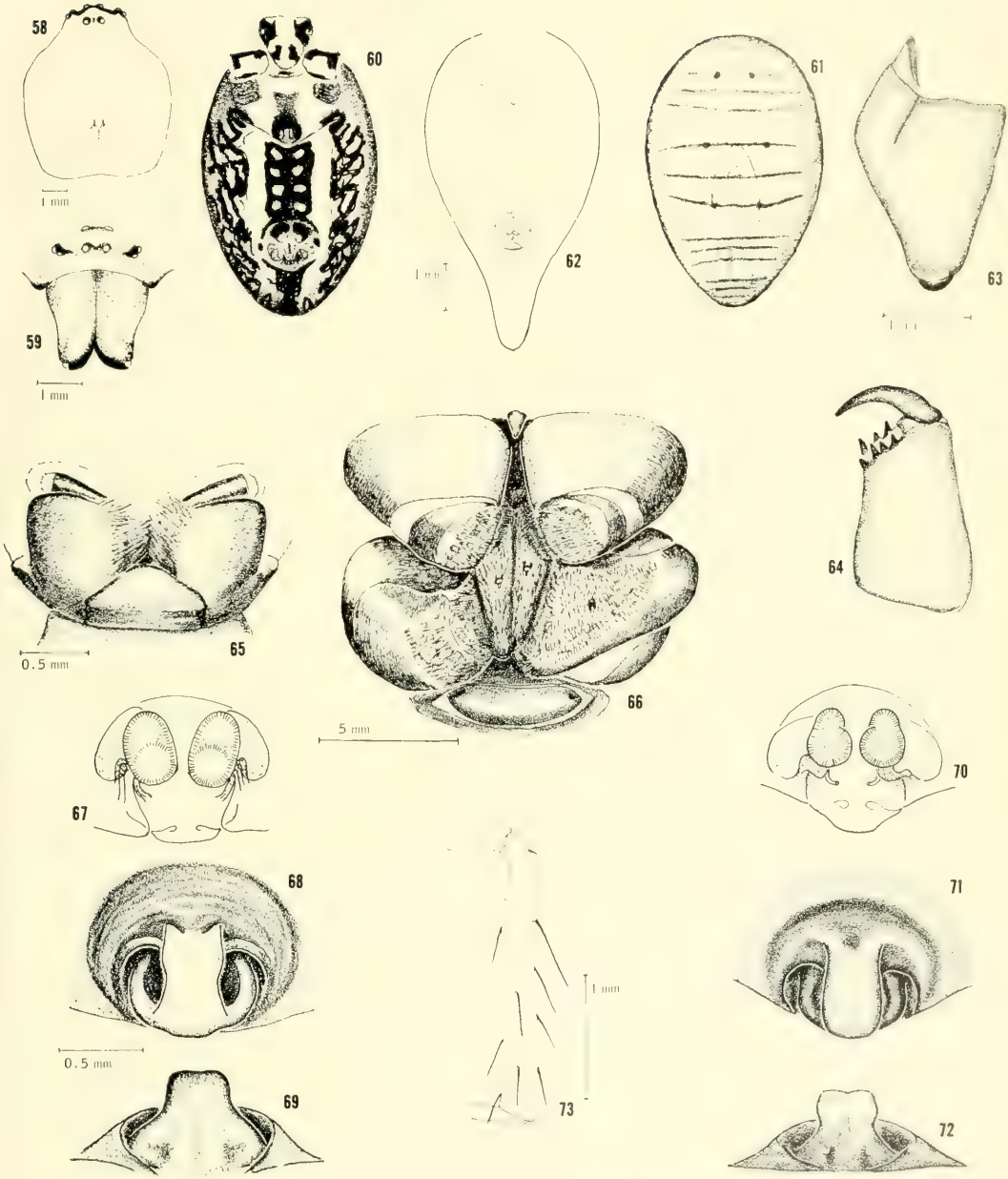
Palpus. The palpi of *Gea* and *Argiope* consist of the same parts seen in theridiid palpi (Figs. 39, 42). When I started to work on the family Theridiidae, I named the parts following other authors. It would have been wiser to study first the araneid palpi on which the anatomical names were based during the 19th century. I find now that what I called median apophysis in the theridiid palpus is not at all the same structure called median apophysis by Chyzer and Kulczynski (1891, *Aranea Hungariae*, Budapest, vol. 1) in *Araneus diadematus*. As the parts of the araneid palpus were named long before those of the Theridiidae, it is necessary to change the names used for theridiid palpi to make them correspond; that is, to exchange the term median apophysis for radix and vice versa. The mistake was made presumably because the theridiid radix often is similar in appearance to the median apophysis of the Araneidae. Such similarity of two nonhomologous structures suggests similar function. The figure (fig. 12) I published of *Araneus* palpi (Levi, 1961, J. Morphol. 108: 4) after Comstock was poorly copied and incorrectly labelled.

On the mesal side of the palpus (Figs. 39–42) in *Argiope* and *Gea* is the radix (R) as in theridiids. The median apophysis (M) is a median structure seemingly of no function but of complex shape that differs in different species. In all *Argiope* and *Gea* the embolus (E) is large and lies within a large conductor (C). As in other Araneidae, there is an additional sclerite, the stipes (I), between the radix and the base of the embolus. But the terminal apophysis found in the palpi of *Araneus* species is lacking.

Growth. Crome and Crome (1961a) published the remarkable observation, based on sampling in the field, that the body of female *Argiope bruennichi* doubles its size after copulation without any intervening molt. Individuals with a large abdomen (ready to lay eggs) had a longer carapace and longer legs than individuals with a small abdomen (which presumably had just molted). There is some possibility that the observation is erroneous.

Crome indicated that this growth is allometric. However, plotting of Crome's own data on graph paper indicated that the growth is proportional.

A female *Argiope argentata* kept in the laboratory here had its first left leg removed 18 days after the last molt. The virgin female spider died 5½ months later of natural death. There were no measurable differences between the remaining right leg and the preserved leg. The female was the normal size of adult *A. argentata*, and all parts grew in the same proportion during the last molt (the skin was kept). The experiment was designed and carried out by W. Eberhard to test the Crome ob-



Argiope trifasciata (Forskål). Figs. 58–72. Female. Fig. 58. Carapace. Fig. 59. Eyes and chelicerae. Figs. 60–62. Abdomen. 60. Ventral view. 61. Dorsal view. 62. Ventral view from St. Croix, Virgin Islands. Figs. 63–64. Left chelicera. 63. Lateral view. 64. Posterior view. Fig. 65. Endites and labium. Fig. 66. Spinnerets. Figs. 67–69. Epigynum from Egypt. 67. Dorsal view. 68. Ventral view. 69. Posterior view. Figs. 70–72. Epigynum from Ontario. 70. Dorsal view. 71. Ventral view. 72. Posterior view.

Argiope argentata (Fabricius). Fig. 73. Male, prolateral view of patella and tibia of first left leg.

servations on one individual of another species.

Relationships. A number of characters including the large size and long metatarsi suggest relationship with *Nephila*. More likely both are adaptations to the habit of hanging in the web (Plates I, II) as the genitalia of the spiders and the structure of the web are quite different.

Among the species of *Argiope*, *A. trifasciata* (Figs. 60, 61) looks superficially much like *A. bruennichi*. *Argiope trifasciata*, although cosmopolitan, has not been collected with *A. bruennichi* and is not found in Europe; their ranges are mutually exclusive. However, the genitalia of the two species are quite different. The genitalia of the European *A. bruennichi* (Figs. 40, 41) are similar to those of *A. aurantia* (Figs. 56, 57), but the two are quite different in coloration. All other American species have genitalia similar to those of *A. trifasciata*, so similar that species may at times be difficult to separate on the basis of genitalia only. These other similar species are all sympatric with *A. trifasciata* but probably are limited to different habitats. Other *Argiope* similar to *A. trifasciata* are found in New Guinea and the East Indies (Chrysanthus, 1958, 1961). But, of course, the *Argiope* of India and Africa are not well known.

Most similar to *A. trifasciata* in coloration is *A. florida*. *Argiope florida* (Figs. 95–97) has some color characteristics found in juveniles (and males) of *A. argentata* (Figs. 128). There is some evidence of character displacement; the genitalia of *A. trifasciata* are noticeably small (Figs. 80–85) in those parts of the range where *A. florida* occurs. *Argiope florida* is found only in the southeastern United States. The three species, *A. argentata*, *A. savignyi* and *A. blanda* have similar color, similar genitalia and are sympatric; their habits are not known.

Habits. In connection with the habit of hanging in the middle of the web in broad daylight, often in the sun, one finds several characteristics that may be adaptive. The silver reflecting pigment, for instance, is found in some other Araneidae that hang in the web at daytime (e.g. *Leucauge*, *Tetragnatha*), also in the web parasites *Argyrodes* of the family Theridiidae. The large size may be an adaptation against water loss (the surface is relatively small compared to the volume). The long metatarsi are otherwise found only in *Nephila* which has similar habits and is also large, while the very different web and genitalia indicate that *Nephila* is not closely related to *Argiope*.

All species probably prey mainly on grasshoppers. I have observed more grasshoppers caught in an *A. trifasciata* web than the spider could possibly consume. Argiopes live less than a year; the female dies after making an egg-sac.

Studies on the life history and behavior of the European *Argiope bruennichi* have been made by Crome and Crome (1961a, b). Information on American species can be found in McCook (1889–1894), and observations on various species of *Argiope* have been published by Lewis and Eve (1965), Peters (1953), Richter (1960), and Wiehle (1931).

Misplaced Species

Argiope marxii McCook, 1894, American Spiders, 3: 223, pl. 1, fig. 5, ♀. Female holotype from Fort Yuma [Yuma], Arizona, in the U.S. National Museum, examined, [= *Cyrtophora molluccensis* (Doleschall)]. It was collected by Marx; as many of Marx's collecting labels are in error, we cannot be certain that the specimen actually came from Yuma. Another female of *Cyrtophora molluccensis* from Albu-

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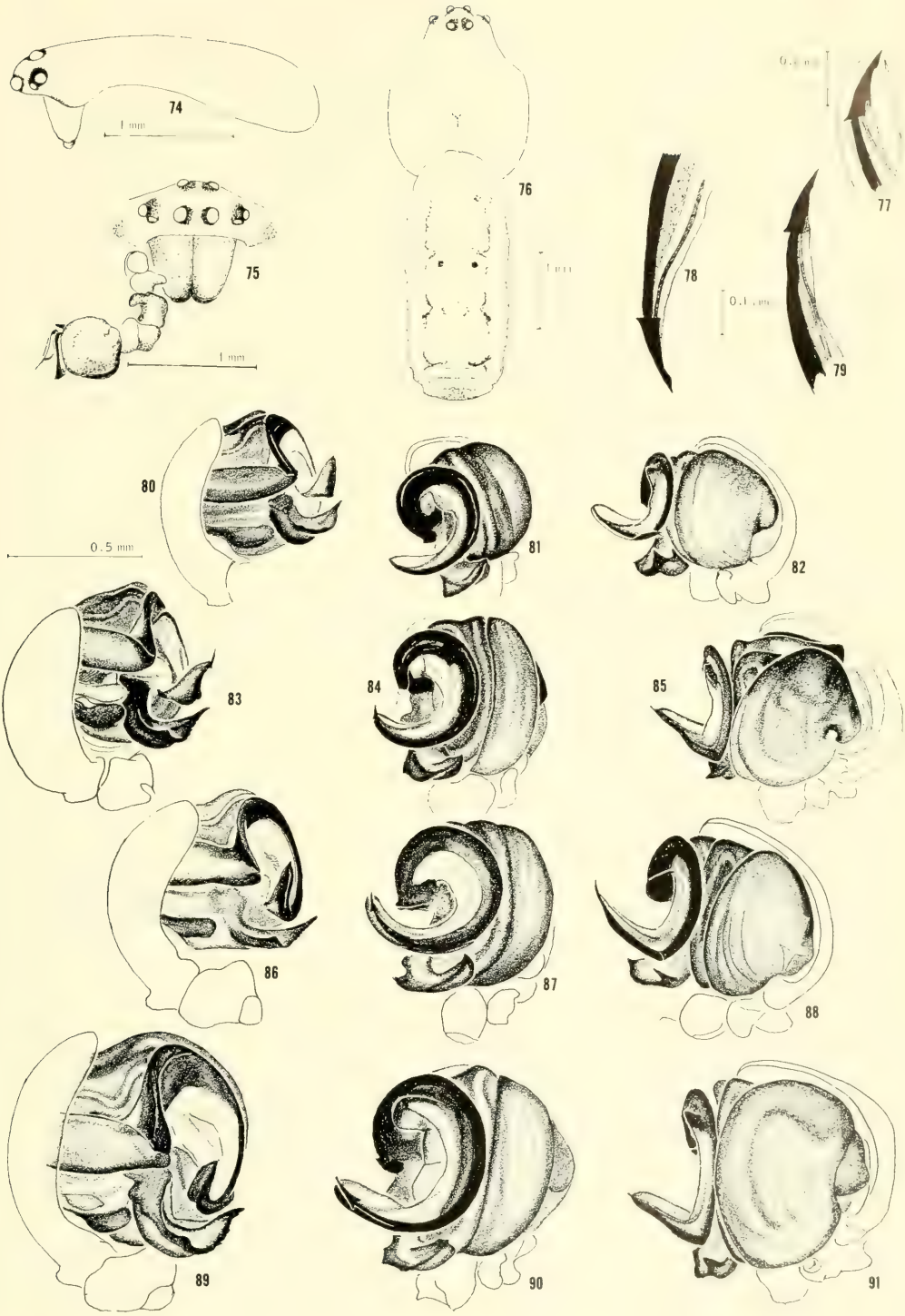
Argiope trifasciata (Forskål), male. Fig. 74. Carapace and chelicera. Fig. 75. Eyes, chelicerae and palpus. Fig. 76. Dorsal view. Figs. 77–79. Left embolus tip. 77. Egypt. 78–79. California. Figs. 80–91. Left palpus. 80–85. Florida. 86–88. Ontario. 89–91. Egypt. 80, 83, 86, 89. Mesal view. 81, 84, 87, 90. Ventral view. 82, 85, 88, 91. Ectal view.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querque, Arizona [*sic*] is in the Museum of Comparative Zoology, Banks collection.

Epeira fascinatrix Walckenaer, 1841, Histoire Naturelles des Insectes Aptères, 2: 111. Female holotype from Rio de Janeiro, collected by Freycinet, lost. This name may have to be applied to the common very large araneid found in the gardens of Rio de Janeiro. It is not an *Argiope*, but I am not certain to which genus the species belongs.

Key to North American *Argiope*

Females

1a. Venter of abdomen with a white transverse band (Fig. 125); tropical species ... 2
1b. Venter of abdomen without white transverse band (Figs. 51, 160); temperate and tropical species ... 3
2a. Transverse band almost as wide as black area between band and epigynum (Fig. 144); posterior face of epigynum narrow without depressions (Fig. 142); Texas to Guatemala ... *blanda*
2b. Transverse band less than half width of black area anterior to it (Fig. 125); posterior face of epigynum relatively wide and with two depressions on its surface (Fig. 122); widespread, tropical ... *argentata*
3a. Sides of posterior half of abdomen lobed ... 4
3b. Sides of posterior half of abdomen without lobes ... 5
4a. Posterior half of dorsum of abdomen with two longitudinal parallel lines (Fig. 97); southeastern United States ... *florida*
4b. Posterior third of dorsum of abdomen almost entirely black (Fig. 161); Costa Rica to Bolivia ... *savignyi*
5a. Dorsum of abdomen black with yellow spots (Fig. 52) ... *aurantia*
5b. Dorsum of abdomen silvery with some transverse black lines, sometimes with some yellowish or orange marks (Fig. 61) ... *trifasciata*

Males

1a. Various sclerites projecting out from cymbium making the palpus much wider than long (Figs. 56, 57) ... *aurantia*
1b. Sclerites of palpus not projecting but more or less curled ... 2
2a. A small spur near tip of palpal embolus (Figs. 130–133, 135, 136) ... *argentata*
2b. No spur near tip of embolus ... 3
3a. A large spur present on the distal face of the median apophysis (Figs. 149, 165); tropical America ... 4
3b. No spur or only a small spur (Fig. 106) on distal face of median apophysis ... 5
4a. A large thorn at base of palpal embolus (Figs. 149–151); Texas to Guatemala ... *blanda*
4b. Without thorn at base of palpal embolus (Figs. 165–167); Costa Rica to Bolivia ... *savignyi*
5a. Diameter of palpus greater than 0.6 mm; coil of embolus large, tip almost straight (Figs. 107, 110); southeastern United States ... *florida*
5b. Diameter of palpus less than 0.5 mm; coil of embolus small, tip curved (Figs. 81, 84, 87, 90); Canada to Chile ... *trifasciata*

Argiope lobata (Pallas) Lobed Argiope

Figures 25–38

Aranea lobata Pallas, 1772, Spicilegia Zoologica, 9: 46. Holotype from unknown locality [presumably from the Ukraine], lost.

Argiope lobata,—Simon, 1870, Ann. Soc. Entomol. France, (4) 10: xcv. Kolosváry, 1938, Zool. Anz., 123: 22–25. Bonnet, 1955, Bibliographia Araneorum, 2: 687. Levi and Levi, Spiders and their Kin, p. 69 (in press).

The name *Argiope lobata* is applied to the common Mediterranean species found also in southern Russia. I have examined specimens from Kazakhtan, Kazakh, USSR, France and North Africa. No two looked alike (Figs. 25–35) and all seemed sufficiently different to be considered different species on first impression. However, large series of the spiders were examined by Kolosváry (1938) who illustrated 83 different epigyna showing all kinds of intergrades. There seems to be both geographical and individual variation. Kolosváry, in one of the few studies of variation of European spiders, considered all of them to

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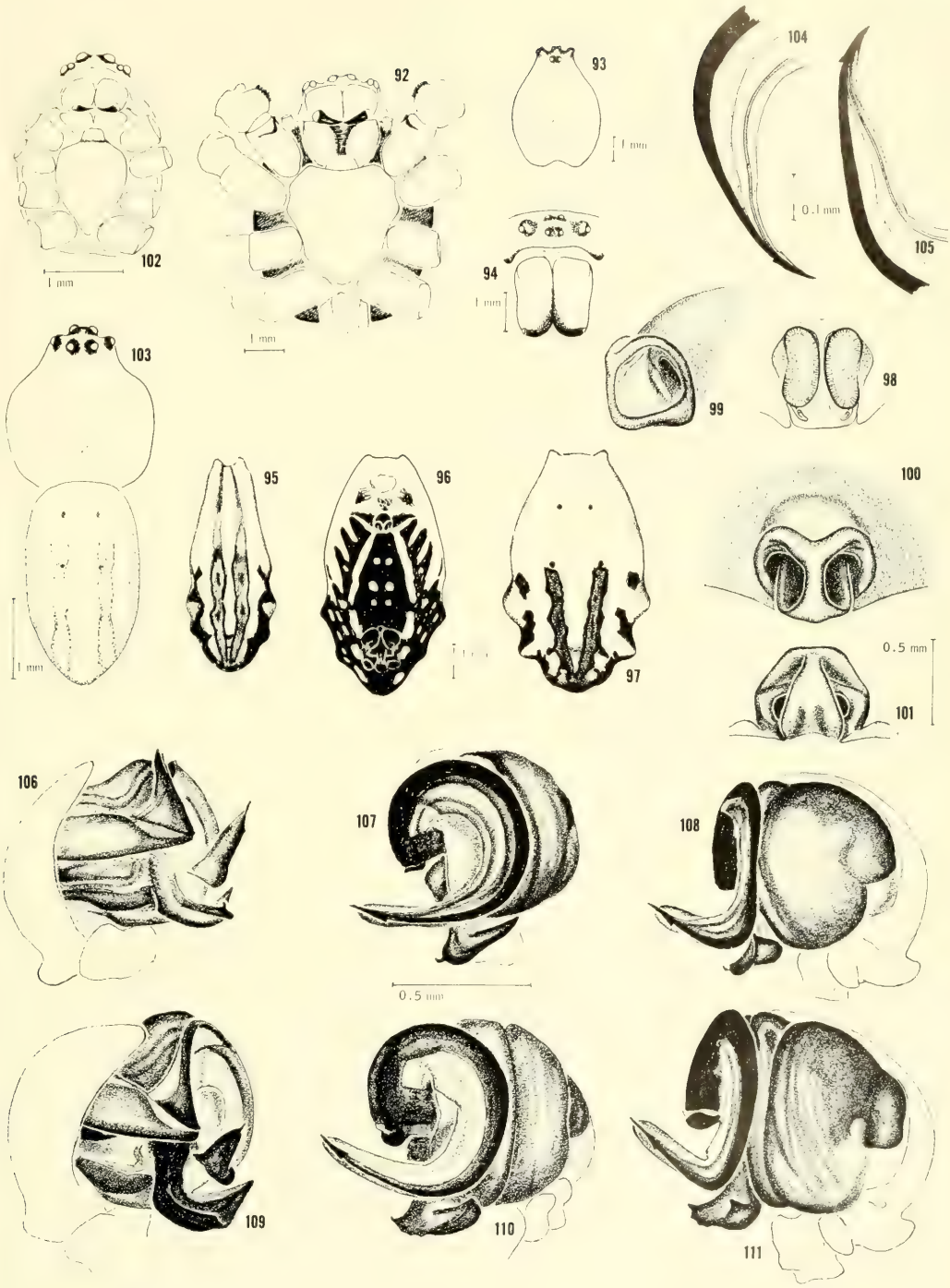
Argiope florida Chamberlin and Ivie. Figs. 92–101. Female. 92. Sternum and coxae. 93. Carapace. 94. Eyes and chelicerae. 95. Abdomen of juvenile female. 96. Ventral view of abdomen. 97. Dorsal view of abdomen. 98–101. Epigynum. 98. Dorsal view. 99. Lateral view. 100. Ventral view. 101. Posterior view. Figs. 102–111. Male. 102. Sternum and coxae. 103. Dorsal view. 104, 105. Tip of left embolus. 106–111. Left palpus. 106, 109. Mesal view. 107, 110. Ventral view. 108, 111. Ectal view.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belong to one species. His argument is convincing.

The species has a greenish color in alcohol. Color slides made available by Mr. R. König show that the dorsum of the carapace and abdomen (Fig. 36) is silvery in living specimens (Levi and Levi, in press).

Argiope aurantia Lucas
Black and Yellow Argiope
Figures 43–57; Map 2

Argyope aurantia Lucas, 1833, Ann. Soc. Entomol. France, 2: 86, pl. 5, fig. 1, ♀. Female holotype from North America probably in the Muséum National d'Histoire Naturelle, Paris. Not seen.

Nephila vestita C. L. Koch, 1839, Die Arachniden, 5: 35, pl. 358, ♀. Female holotype, locality unknown, presumably in the Berlin Museum.

Epeira cophinaria Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 109. Holotype, Abbot illustration no. 151, from Georgia, in British Museum; color photograph of original examined.

Epeira ambitoria Walckenaer, 1841, *ibid.*, 2: 112. New name for *Nephila vestita* Koch from New York.

Epeira riparia Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 468, pl. 30, fig. 5, ♀. Female holotype from United States, lost.

Epeira sutrix Hentz, 1847, *ibid.*, 5: 478, pl. 31, fig. 23, ♀. Juvenile female syntypes from South Carolina and Pennsylvania, lost.

Argiope riparia, Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 329, pl. 34, fig. 19, ♀, pl. 38, figs. 13, 14, 19, ♀♂.

Argiope riparia var. *multiconcha* Treat, 1887, Amer. Natur., 21: 1122. Female holotype from Guthrie, Missouri.

Argiope personata O. P.—Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1: 110, pl. 14, fig. 14, ♀. Female holotype from Acapulco, Mexico, in the British Museum.

Argiope cophinaria,—McCook, 1893, American Spiders, 3: 217, pl. 15, figs. 1–6; pl. 16, figs. 1, 5, 6, ♀♂.

Argiope aurantia,—Simon, 1895, Histoire Naturelles des Araignées, 1: 765, 767. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 221, figs. 717–721. Bonnet, 1955, Bibliographia Araneorum, 2: 675. Levi and Levi, Spiders and their Kin, p. 69 (in press).

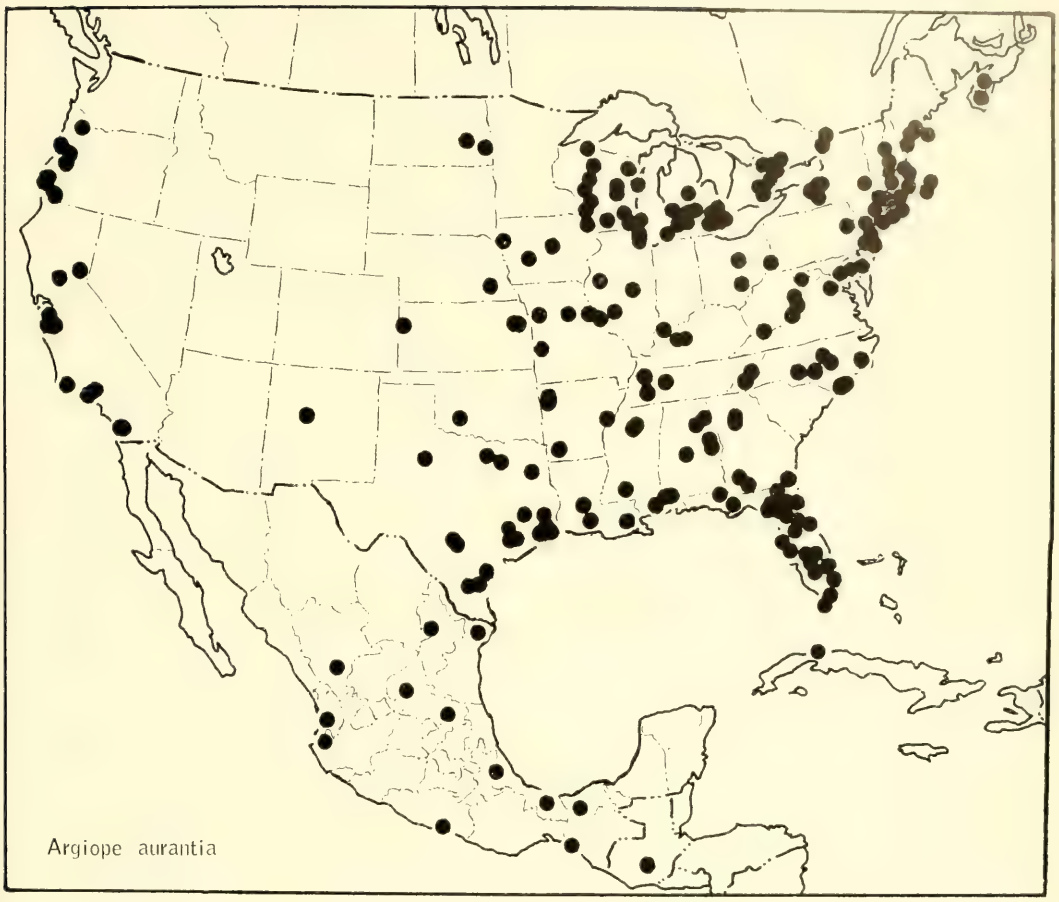
Argiope godmani O. P.–Cambridge, 1898, Biologia Centrali-Americana, Araneidea, 1: 236, pl. 37, fig. 8. Female holotype from Guatemala City, Guatemala, in the British Museum.

Miranda cophinaria,—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 452, pl. 43, figs. 4, 5, ♀♂.

Description. Male, specimen described from Michigan. Carapace brown with white hairs. Sternum black with white median longitudinal band. Legs brown. Dorsum of abdomen black with an indistinct yellow-white longitudinal band on each side (Fig. 54). Venter black with two indistinct longitudinal lines. Anterior median eyes about one and one-half diameters apart, one diameter from laterals; posterior median eyes one and one-half diameters apart, two diameters from laterals. Sides of abdomen almost parallel to each other (Fig. 54). Total length 5.5 mm. Carapace 2.7 mm long, 1.8 mm wide. First femur, 4.3 mm; patella and tibia, 5.0 mm; metatarsus, 5.0 mm; tarsus, 1.5 mm: Second patella and tibia, 4.8 mm; third, 2.4 mm; fourth, 3.9 mm.

Female, specimen described from Michigan. Carapace yellow-white with some brown markings covered up by white hair, eye region black. Sternum black with median longitudinal yellow-white band (Fig. 51). Legs are banded dark brown; the brown bands are wider than in-between light areas. Dorsum of abdomen is shiny black with yellow markings (Fig. 52). Venter with two longitudinal white bands enclosing four small pairs of white spots on black (Fig. 51). Anterior median eyes about one and one-half diameters apart, one and one-half diameters from laterals; posterior median eyes two diameters apart, three diameters from laterals. Abdomen is shield-shaped with two anterior projections. Total length 18 mm. Carapace 15.9 mm long, 4.3 mm wide. First femur, 7.4 mm; patella and tibia, 8.0 mm; metatarsus, 6.8 mm; tarsus, 1.8 mm. Second patella and tibia, 7.6 mm; third, 4.3 mm; fourth, 7.2 mm. Range of size of females between 14 and 25 mm. Largest specimens are from the Southwest and Mexico.

Diagnosis. The species is closest to the European *A. bruennichi*, which has a similar palpus and (Figs. 39–41) also has an epigynum with a scape, but *A. bruennichi* has the coloration of *Argiope trifasciata*



Map 2. Distribution of *Argiope aurantia* Lucas.

(Fig. 61) while *A. aurantia* is brightly colored yellow and black (Fig. 52).

Habits. Males are mature in July and August, females from August to December in Florida. In Wisconsin and Michigan males are mature in August, females presumably from August to October. For New England, Kaston (1948) reported mature males in late July and August, females from August to October with the first cocoons appearing in August and September.

In Florida, all collecting reports with habitat information indicate that the species is limited to margins of lakes, stream banks, near ponds or sinks in swamps, rarely in sand scrub. Also in Michigan at the George Reserve, *A. aurantia* is limited to swamps, bogs and pond margins; this is probably true also for Wisconsin. In New England *A. trifasciata* and *A. aurantia* are found in similar habitats, meadows containing high grass and goldenrod (*Solidago* sp.). Both species were very abundant from 1956 to 1957 but rapidly disappeared with the onset of the recent (1960–1966) drought, *A. aurantia* being first to disappear. Both species reappeared in large numbers during the wet summer of 1967.

The web has a single zig-zag stabilimentum that extends above and below the center. The egg cocoon is a brown sphere of papery consistency attached at its top

end. Each sphere contains 400 to 1000 yellow eggs. Young instars overwinter in the egg cocoon and emerge in April or May (Kaston, 1948).

Distribution (Map 2). Nova Scotia, southern Ontario, south to Guatemala City, Guatemala, but absent from predominantly arid areas. There is a literature record from El Salvador (Peters, 1953) indicating that it is found in hot lowlands along the coast, disappearing in fall.

Argiope trifasciata (Forskål)
Banded Argiope

Plate I; Figures 58–72, 74–91; Map 3

Aranea trifasciata Forskal, 1775, Descriptiones Animalium Avium, Amphibiorum, Piscium, Insectorum, Vermum, Hauniae, p. 86. Holotype from Cairo [Egypt], lost.

Aranea fastuosa Olivier, 1789, Encycl. Méthod., 4: 202. Syntypes from Guadalupe.

Argyope aurelia Audouin, 1827, Explication sommaire des Planches d'Arachnides, *in* Savigny, Description de l'Egypt., 22: 331, pl. 2, fig. 5, ♀ ♂. Syntypes from Egypt.

Epeira webbii Lucas, 1838, *in* Barker, Webb, Berthelot, Histoire Naturelle des Iles Canaries, 2: 38, pl. 6, fig. 5, ♀. Syntypes from Canary Islands.

Epeira argyraspides Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 110. Female holotype is Abbot illustration, fig. 156, in the British Museum; color photograph examined.

Epeira fasciata,—Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 468, pl. 30, fig. 8, ♀. Not *Epeira fasciata* (= *A. bruennichi*).

Epeira flavipes Nicolet, 1849, *in* Gay, Historia Chili, 10 (3): 493. Specimens from Valdivia, Chile, probably in the Muséum National d'Histoire Naturelle, Paris.

Argyope avara Thorell, 1859, Öfvers Kongl. Vet. Akad. Förh., 16: 299. Female syntypes from San Francisco, California, and Oahu, Honolulu, in the Natural History Museum, Stockholm, examined. The California specimen is in poor condition, the Hawaiian specimen in excellent physical condition. Bonnet, 1955, Bibliographia Araneorum, 2: 677 (sub *Argiope*). NEW SYNONYMY.

Argiope trifasciata,—Thorell, 1873, Remarks on Synonyms of European Spiders, p. 519. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv. 70: 222, figs. 697–699, 722–723, 2034–2035, ♀ ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 694. Levi and Levi, Spiders and their Kin, p. 68. (in press)

Argiope sticticalis O. P.-Cambridge, 1876, Proc. Zool. Soc. London, p. 576. Juvenile syntypes from Egypt probably at the Hope Dept. of Entomology, Oxford.

Argyopes indecissa Holmberg, 1876, An. Agr. Rep. Argentina, 4: 112. Female specimens presumably from Buenos Aires, lost.

Argiope hentzi Thorell, 1878, Ann. Mus. Civ. Genova, 13: 295. New name for *A. fasciata*, —Hentz.

Argiope transversa Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 330, pl. 34, fig. 20; pl. 28, figs. 15–18, ♀ ♂. New name for *A. fasciata*,—Hentz.

Argiope argyraspis,—McCook, 1894, American Spiders, 3: 219, pl. 15, figs. 7–12; pl. 16, figs. 3–4, ♀ ♂.

Metargyope trifasciata,—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 451, pl. 43, figs. 2, 3, ♀ ♂

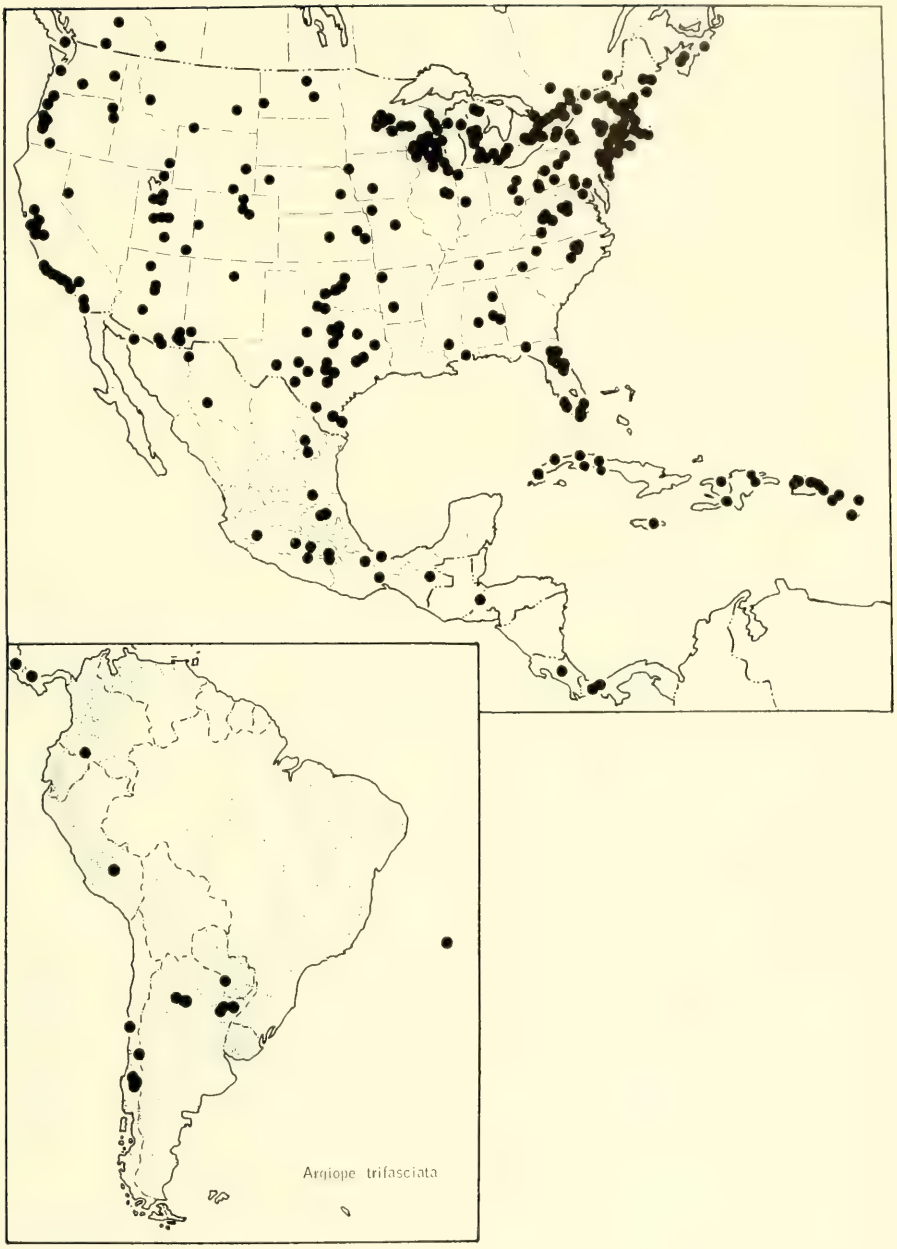
Argiope simplex Badcock, 1932, J. Linnean Soc. London, 38: 17, fig. 12. Female holotype from Rio Verde, 6 miles north of Makthlawaiya, Paraguay, in the British Museum, examined by D. J. Clark. NEW SYNONYMY.

Argiope abalosi Mello-Leitão, 1942, Rev. Mus. La Plata, (N.S.) 2: 399. Juvenile holotype from Luján, Santiago del Estero in the Museo de la Plata, examined. NEW SYNONYMY.

Argiope seminola Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8 (5): 96, figs. 98–102, ♀ ♂. Female holotype from 10 miles east of Naples, Florida, probably in the University of Utah collection, not seen. NEW SYNONYMY.

Argiope stenogastra Mello-Leitão, 1945, Rev. Mus. La Plata, (N.S.) 4: 235. Juvenile holotype from Solari, Corrientes, in the Museo de la Plata, examined. NEW SYNONYMY.

Description. Male, specimen described from North Carolina. Carapace yellow-brown. Sternum yellow-brown with white spot opposite each coxa surrounded by some dark pigment. A white spot behind labium. Legs yellowish brown. Dorsum of abdomen white. Venter with pigment spots and two white lines bordered by narrow black ones. Anterior median eyes about one and one-half diameters apart. Posterior eyes a little more than two diameters apart. Sides of the abdomen almost parallel (Fig. 76). Total length 5.5 mm. Carapace 3.0 mm long, 2.1 mm wide. First femur, 4.6 mm; patella and tibia, 5.8 mm; metatarsus, 5.6 mm; tarsus, 1.6 mm. Second patella and tibia, 5.0 mm; third, 2.0 mm; fourth, 4.2



Map 3. American distribution of *Argiope trifasciata* (Forskål).

mm. Total length of a male from the West Indies 5.8 mm. Carapace 2.7 mm long, 2.3 mm wide. First patella and tibia, 4.3 mm; second, 4.0 mm; third, 1.7 mm; fourth, 3.1 mm.

Female, specimen described from North Carolina. Carapace dark with white scales. Sternum black with a median white longitudinal band and two white spots on each side (Fig. 60). Legs dark brown with dark brown bands as wide as lighter areas between. Abdomen white with transverse dark lines (Fig. 61). Venter black with two parallel white lines enclosing a black area which contains four pairs of white spots (Fig. 60). Anterior median eyes one and one-quarter diameters apart, one and one-half diameters from laterals. Posterior eyes a little less than two diameters apart. Abdomen oval in shape, sometimes posterior tip overhanging way beyond the spinnerets (Fig. 62). Total length, 17 mm. Carapace 5.5 mm long, 4.0 mm wide. First femur, 7.6 mm; patella and tibia, 8.2 mm; metatarsus, 8.2 mm; tarsus, 2.1 mm. Second patella and tibia, 8.1 mm; third, 4.2 mm; fourth, 7.0 mm.

Total length of a female from the West Indies 24 mm. Carapace 7.4 mm long, 6.3 mm wide. First femur, 10.1 mm; patella and tibia, 11.0 mm; metatarsus, 12.5 mm; tarsus, 2.4 mm. Second patella and tibia, 11.0 mm; third, 5.9 mm; fourth, 8.9 mm.

Variations. Females range in size from 12–26 mm. The smallest specimens came from southern South America, the largest ones from the West Indies and Mexico. The West Indian specimens had the most overhanging tails (Fig. 62).

Diagnosis. Male *Argiope trifasciata* have been confused with *A. florida*. However, the embolus has a diameter of less than 0.5 mm (Figs. 81, 84, 87, 90); that of *A. florida* is more than 0.6 mm (Figs. 107, 110). The embolus lacks the small spur that projects near the tip in *A. argentata* (Figs. 130–133). Females can be separated from other species by lack of a transverse lip anterior to the septum of the epigynum (Figs. 68, 71).

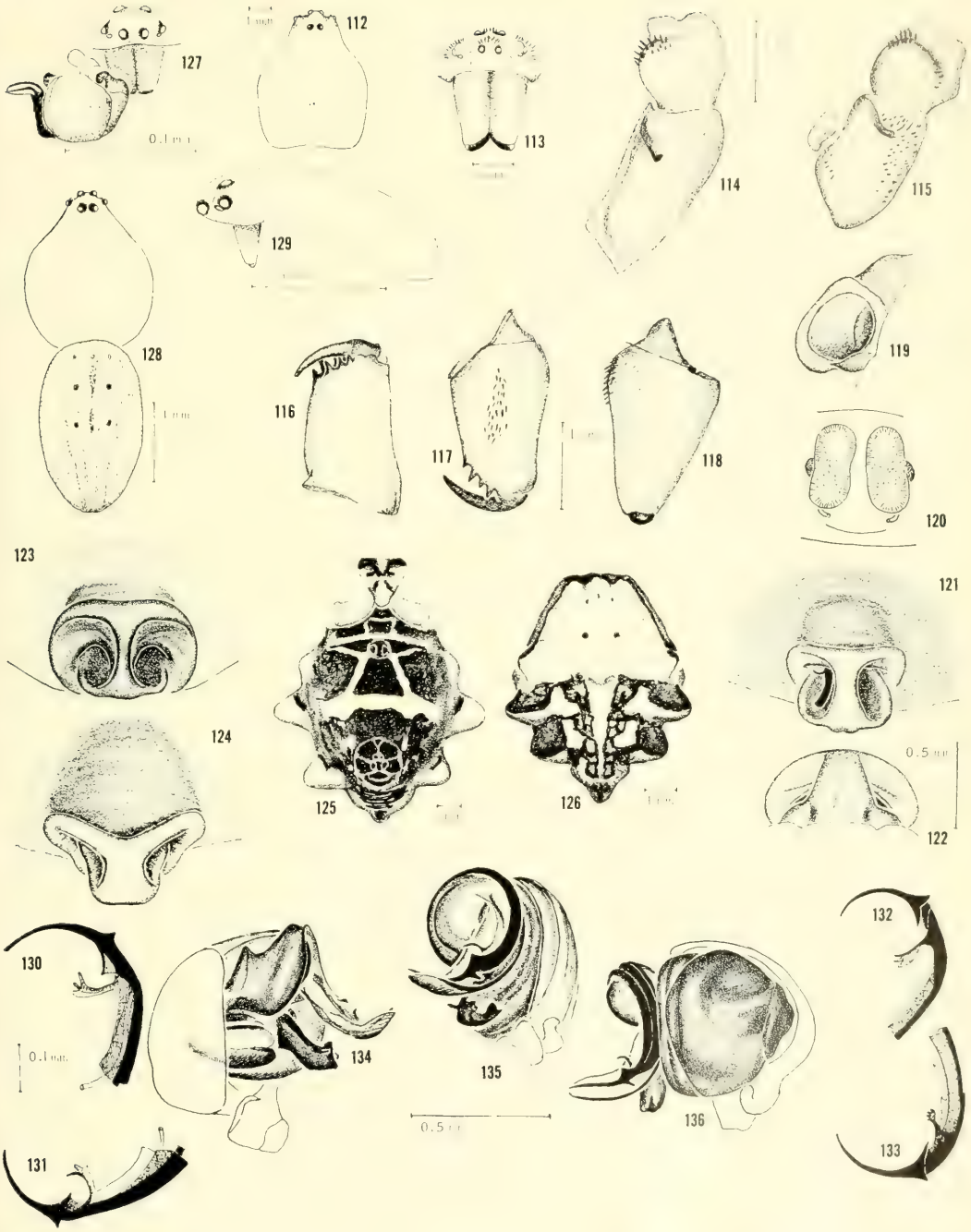
Habits. Males are mature from June until November in Florida, females from June until December. In Wisconsin and Michigan males are found from August until September, females from August until October. In Connecticut, males are mature from July to September, females from August until frost (Kaston, 1948); the dates are about the same in other parts of New England.

In Florida the animals are found in high dry grass areas and weeds, in low brush in pines, in sand scrub, all much drier habitats than that of *A. aurantia*. All collections in Michigan came from upland fields, rarely moist fields. Kaston (1948) reports *A. trifasciata* and *A. aurantia* from similar situations but less common than *A. aurantia* in Connecticut. In the areas of eastern Connecticut and eastern Massachusetts that I have lived in, *A. trifasciata* was more common than *A. aurantia* but had similar habitats. While both species were very common in 1956–1957, both almost disappeared, perhaps as a result of the recent (1960–1966) drought. Individuals of *A. trifasciata* were found occasionally during the drought. They reappeared in abundance during the summer of 1967.

In large collections from the West Indies, *Gea heptagon* was commonly collected with *Argiope argentata*. But *Gea* and *A. trifasciata* were never collected together.

→

Argiope argentata (Fabricius). Figs. 112–125. Female. 112. Carapace. 113. Eyes and chelicerae. 114–115. First left coxa and trochanter. 116–118. Left chelicera. 116. Posterior view. 117. Anterior view. 118. Lateral view. 119–124. Epigynum. 119–122. Veracruz, Mexico. 119. Lateral view. 120. Dorsal view. 121. Ventral view with embolus tip. 122. Posterior view. 123. Ventral view from slightly posterior, Florida. 124. Ventral view, Lima, Peru. 125. Abdomen, ventral view. 126. Abdomen, dorsal view. Figs. 127–136. Male. 127. Eyes, chelicerae and palpus. 128. Dorsal view. 129. Lateral view of carapace. 130–132. Embolus tips. 130, 131. From right side of epigynum, from Peru. 132–133. Right tips, Mexico. 134–136. Left palpus. 134. Mesal view. 135. Ventral view. 136. Lateral view.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The web has a vertical stabilimentum above and below the spider; sometimes it is lacking (Kaston, 1948). The egg-sac is made in fall and soon afterward the female dies. The sac is brown, the eggs yellow, more than 100 of them in a sac (Kaston, 1948). In New England there is just one generation a year. The egg-sac is papery, flat above and rounded below. The young spiderlings in spring resemble young tetragnathids but do not have long jaws and the venter of the abdomen has a black longitudinal band.

Distribution. Cosmopolitan but absent from areas where *A. bruennichi* is found. It has been reported from the Mediterranean, Angola and Natal, Madagascar, Asia Minor, Indian Ocean islands, Malay Peninsula, Australia, New Caledonia, New Hebrides, Fiji (Bonnet, 1955). In the Americas, it occurs from Nova Scotia and British Columbia, to southern Chile and northern Argentina, and Hawaii, but apparently it is absent from large areas that are covered by tropical forests (Map 3).

The distribution of *A. trifasciata* is unknown, because it may have been confused with *A. bruennichi* of Eurasia and other names may have been applied to it. It appears to be almost cosmopolitan. Specimens examined from the Mediterranean region came from Madeira, Porto Santo (T. D. A. Cockerell). African specimens examined were from Egypt; and from Faradje, Republic of the Congo (American Museum Congo Expedition). Atlantic Ocean islands: Madeira, Isla da Trinidade (Brazil) and St. Helena Island (A. Loveridge). It is a common species on St. Helena. Australian Pacific area: Eromanga Island, New Hebrides (L. MacMillan), Western Australia (B. Y. Main).

There are literature records from the lower Amazon (F. P.-Cambridge, 1903) and Guyana, Brazil, and the Antarctic (Bonnet, 1955). The Antarctic record turned out to be an error: it was collected by the British Expedition to the Antarctic Continent on Trinidad Island off the coast of Brazil. No spiders are known from the Antarctic.

Argiope florida Chamberlin and Ivie
Florida Argiope

Plate II; Figures 92–111; Map 4

Argiope argentata,—McCook, 1894, American Spiders, 3: 220 (in part), pl. 16, fig. 1, ♀. Not *A. argentata* (Fabricius).

Argiope florida Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8 (5): 95, figs. 93, 94, 96, ♀. Female holotype from Lake Worth, Florida, found in webs of large cacti probably in the University of Utah collection, not seen.

Argiope seminola,—Chamberlin and Ivie, 1944, *ibid.*, 8 (5): 96, figs. 100, 102, ♂. Not ♀ holotype.

Note: The male figured by Chamberlin and Ivie as *A. florida* seems to be a specimen of *A. trifasciata*; the male figured as *A. seminola* is *A. florida*. Figure 551 of Abbot, interpreted as *A. seminola* (= *A. trifasciata*) by Chamberlin and Ivie, is no doubt *A. florida*. The species seems to have been confused with *A. argentata*.

Description: Male. Carapace light brown. Labium, maxillae brown. Sternum dark on each side, legs brown. Abdomen dorsum with two longitudinal bands on some silver (Fig. 103), venter black with two white longitudinal bands. There are no lobes on the sides of the abdomen (Fig. 103). Total length, 4.5 mm. Carapace 2.2 mm long; 2.1 mm wide. First femur, 3.5 mm; patella and tibia, 4.2 mm; metatarsus, 4.0 mm; tarsus, 1.3 mm. Second patella and tibia, 3.8 mm; third, 1.8 mm; fourth, 2.9 mm.

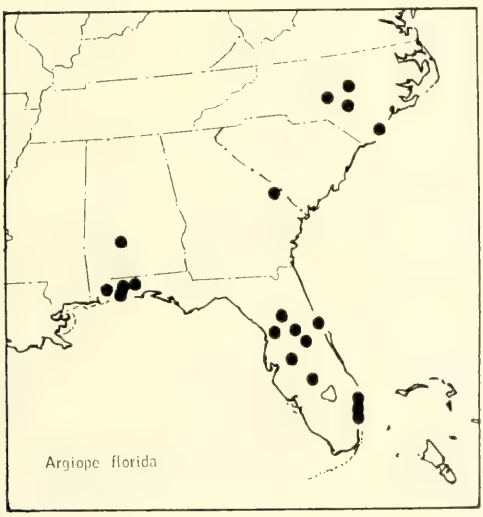
Female. Carapace completely covered by long silvery scales on dark brown background. Chelicerae, labium, maxillae dark brown with labium and maxillae having the distal rim light. Sternum dark brown with median light mark which forks posteriorly into 3 prongs. Legs dark brown with lighter rings as wide as dark areas and some white scales on venter. Dorsum of abdomen silvery with silvery scales on white background except two longitudinal dark stripes at the posterior half of the abdomen (Fig. 97), and the anterior

face of the lateral lobes is black. The venter has two longitudinal white lines on black background, broken in the posterior part of the abdomen and going around spinnerets. Total length, 16 mm. Carapace 10 mm long, 8.0 mm wide. First femur, 8.1 mm; patella and tibia, 8.7 mm; metatarsus, 8.2 mm; tarsus, 2.3 mm. Second patella and tibia, 8.6 mm; third, 5.0 mm; fourth, 7.6 mm.

Diagnosis: Females are easily recognized by the posterior lateral lobes on the abdomen and the two dark dorsal lines (Fig. 97). The anterior edge of the epigynum has a lip (Fig. 100) while that of *A. trifasciata* (Figs. 68, 71) does not. The palpus of the male (Figs. 107, 110) has a diameter of more than 0.6 mm, that of *A. trifasciata* less than 0.5 mm (Figs. 81, 84, 87, 90). It lacks the spur near the tip of the embolus of *A. argentata*.

Habits: The males mature from June to October, the females from July to November. The webs are found in dry sand scrub in longleaf pine and oak-pine flat woods in Florida. There are four stabilimenta in form of a cross (Plate II) as in *A. argentata*.

Distribution: From North Carolina, Alabama, to southern Florida (Map 4).



Map 4. Distribution of *Argiope florida* Chamberlin and Ivie.

Argiope argentata (Fabricius)
Silver Argiope

Plate I; Figures 42, 73, 112–136; Map 5

Aranea argentata Fabricius, 1775, Systema Entomologiae, p. 433. "Habitat in Indiis," type specimens lost. Martini and Goeze, 1778, *in* D. M. Lister, Naturgeschichte der Spinnen, p. 248, "Indianische Silberspinne" [American Indian silver spider]. Fabricius, 1781, Species Insectorum exhibentes eorum differentias auctorum, 2: 539, "Indiis." Gmelin, 1789, C. A. Linné, Systema Naturae, 1 (5): 2953, "Habitat America australi insulique obversis et India." Olivier, 1789, Araignées *in* Encycl. Méth. Hist. Natur. Ins., Paris, 4: 234, "Elle se trouve aux Indes orientales." Fabricius, 1793, Entomologia Systematica emendata, 2: 414, "Habitat in India."

Aranea mammata De Geer, 1778, Mem. Hist. Insectes, 7: 318, pl. 39, fig. 5. Specimens from Pennsylvania [prob. an error] and figured by Sloane from Jamaica.

Argyopes argentata,—C. L. Koch, 1839, Die Arachniden, 5: 38, pl. 361, from "Südamerika"; Holmberg, 1876, An. Agr. Argentina, 4: 112.

Argyopes fenestrinus C. L. Koch, 1939, *ibid.*, 5: 39, fig. 361. Holotype from South America.

Epeira amictoria Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 119. Holotype from Rio de Janeiro, Brazil.

Plectana sloanii Walckenaer, 1841, *ibid.*, 2: 200. Name for a figure by Sloane, History of Jamaica, pl. 235, fig. 3.

Argyopes hirtus Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 103, pl. 1, fig. 23, ♀. Female syntypes from Lima, Chorillas and Callao, Peru. Female lectotype from Lima, Peru, here designated in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY.

Argyopes maronicus Taczanowski, 1873, Horae Soc. Entomol. Rossicae, 9: 261. Female holotype from St. Laurent de Maroni, French Guiana, in the Polish Academy of Sciences, Warsaw.

Argyopes subtilis Taczanowski, 1873, *ibid.*, 9: 261. Female syntypes from Cayenne, French Guiana, in the Polish Academy of Sciences, Warsaw.

Argiope argentata,—McCook, 1893, American Spiders, 3: 220, pl. 16 (in part), fig. 1 (in part), 2. Bonnet, 1955, Bibliographia Araneorum, 2: 673. Levi and Levi, Spiders and their Kin, p. 69 (in press).

Argiope waughi Simon, 1897, Act. Soc. Sci. Chili, 6: 105. No specimens with this name could be found in the Simon collection (M. Vachon in letter). NEW SYNONYMY.

Argyope argentata,—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 450, pl.

42, figs. 25, 26, ♀ ♂. Roewer, 1942, Katalog der Araneae, 1: 744.

Argiope submaronica Strand, 1915, Arch. Naturgesch. 81A (9): 105. Female holotype from "Joinville, Sta. Catherina, Brasilien," depository unknown. This name was first synonymized with *A. argentata* by Bonnet.

Gea panamensis Chamberlin, 1916, Bull. Mus. Comp. Zool., 60: 243, pl. 19, fig. 8. Male holotype from Panama in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Argiope filiargentata Hingston, 1932, A Naturalist in the Guiana Forest, pp. 132, 372. Trinidad. Hingston neither kept his specimens nor designated types. All his specimens seem to be juvenile *A. argentata*. NEW SYNONYMY.

Argiope cuyunii Hingston, 1932, *ibid.*, pp. 133, 373. Cuyuni River, British Guiana (see above). NEW SYNONYMY.

Argiope filiinfracta Hingston, 1932, *ibid.*, p. 373. Trinidad (see above). NEW SYNONYMY.

Argiope argyrea Badcock, 1932, J. Linnean Soc. London, p. 17. Female holotype from Nanahua, Paraguay, in the British Museum, examined by D. J. Clark. NEW SYNONYMY.

Argiope indistincta Mello-Leitão, 1944, Rev. Mus. La Plata, (N.S.) 3: 328. Male holotype from Rosas Costa, Prov. Buenos Aires, in the Museo de la Plata, examined. NEW SYNONYMY.

Note: Apparently the Fabricius type locality was understood to be America by most of his contemporaries, although this is not at all clear. Considering that for more than 150 years the name has been used for the common tropical American species, this is of academic interest only.

Hingston's diagrammatic illustrations of the web of juvenile *Argiope argentata* (to all of which he gave new names), have unfortunately been reproduced in numerous books including Grassé, P., edit., 1949, *Traité de Zoologie*, 6: 692.

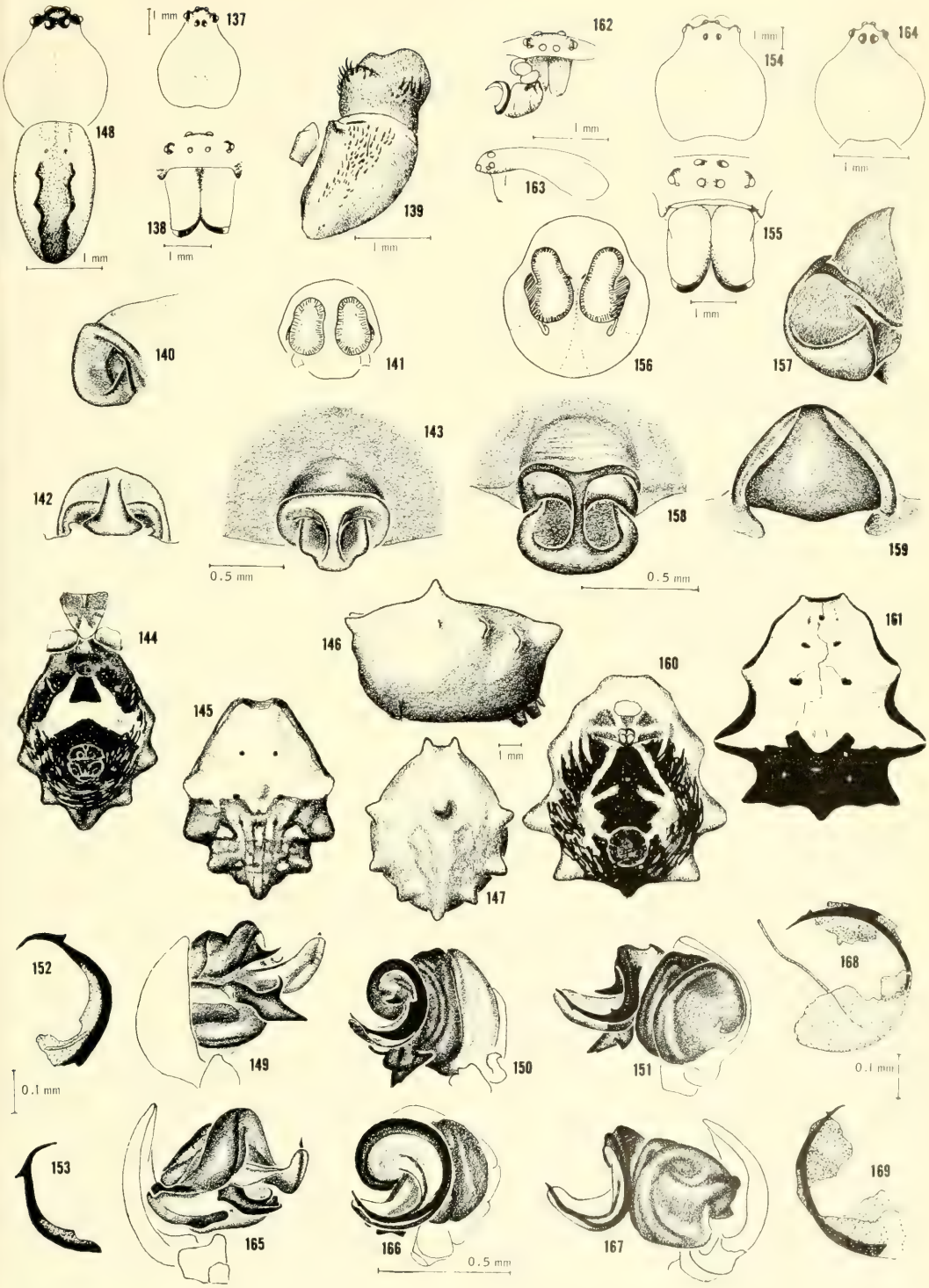
Description. Male specimen described is from St. Croix, British West Indies. Carapace yellow-white with two indistinct longitudinal brownish bands going from each side of eye region, posteriorly, about their width apart. Sternum yellowish white with two longitudinal brown bands, their width apart, a white pigment spot at the base of each coxa. Legs with brown bands slightly wider than intermediate area. Abdomen in alcohol, dorsum whitish with two parallel longitudinal dark bands, their outlines black (Fig. 128). Venter sometimes with dark pigment, generally light with two parallel white lines enclosing but touching a pair of white spots in the middle. Anterior median eyes one diameter apart, three-quarters diameter from laterals. Posterior median eyes one and one-half diameters apart, two diameters from laterals. The abdomen of the male is shield-shaped, pointed behind; there are no tubercles (Fig. 128). Total length 4.0 mm. Carapace 2.4 mm long, 2.0 mm wide. First femur, 2.7 mm; patella and tibia, 3.0 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.5 mm; fourth, 2.1 mm.

Female from the West Indies. Carapace covered completely with white scales that are silver in living specimens. Sternum brown with a median white line. Legs with dark bands. Abdomen in alcohol, anterior white, posterior with a dark pattern containing white spots (Fig. 126). In living specimens, mostly silver. Venter with a transverse white bar which has a width almost one-third length of distance between spinnerets and epigynum; otherwise black, except lateral tubercles whose venter is white. Anterior median eyes one and one-half diameters apart, posterior median eyes

→

Argiope blanda O. P.-Cambridge. Figs. 137–147. Female. 137. Carapace. 138. Eyes and chelicerae. 139. First left coxa and trochanter. 140–143. Epigynum. 140. Lateral view. 141. Dorsal view. 142. Posterior view. 143. Ventral view. 144–147. Abdomen. 144. Venter. 145. Dorsum, pattern. 146. Lateral view. 147. Dorsum. Figs. 148–153. Male. 148. Carapace and abdomen. 149–151. Left palpus. 149. Mesal view. 150. Ventral view. 151. Ectal view. 152–153. Right tip of embolus.

Argiope savignyi new species. Figs. 154–161. Female. 154. Carapace. 155. Eyes and chelicerae. 156–159. Epigynum. 156. Dorsal view. 157. Lateral view. 158. Ventral view. 159. Posterior view. 160. Abdomen venter. 161. Abdomen dorsum. Figs. 162–169. Male. 162. Eyes, chelicerae and palpus. 163. Carapace and chelicera. 164. Carapace. 165–167. Palpus. 165. Mesal view. 166. Ventral view. 167. Ectal view. 168–169. Tip of embolus.


148
1 mm
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0.5 mm
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164
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161
151
168
0.1 mm
167
169

less than two diameters apart. Lateral eyes on higher humps than other species. Abdomen with tubercles around posterior margin (Figs. 125, 126). Total length 12 mm. Carapace 5.7 mm long, 4.6 mm wide. First femur, 6.5 mm; patella and tibia, 9.1 mm; metatarsus, 8.9 mm; tarsus, 1.7 mm. Second patella and tibia, 7.5 mm; third, 5.2 mm; fourth, 7.5 mm.

Variation. There is relatively little variation in size among females of this species.

Diagnosis. The small projection or curl near the tip of the embolus (Figs. 130–133, 135–136) is diagnostic for this species and is not found in any other *Argiope* known to me. Females may be difficult to separate from *A. blanda.* However, Mexican and Central American specimens of *A. argentata* have the posterior face of the epigynum with a depression on each side (Fig. 122), while the posterior face of the epigynum of *A. blanda* is narrower and lacks the depressions. The frequent presence of the broken off, easily identified male embolus tip in the female epigynum facilitates the identification of females.

Habits. Adult males have been collected in February and March and also in June in Florida. The only months for which there are no records of adult females are September and October, but this may reflect the lack of collecting at this season in Florida. It is possible that unlike the temperate species which have only one generation a year, *A. argentata* may have several.

Argiope argentata is found around houses and in gardens, in great abundance at the southern tip of Florida. Its distribution appears to be limited by low temperatures rather than by unsuitable habitat. In the desert of eastern Peru it is found in shrubs along irrigation ditches of stream valleys; in the dry areas of western Argentina it occurs in more moist habitats that provide suitable shrubs for large orb webs.

The web of the adult *A. argentata* has four zigzag stabilimenta forming a cross, the bands going to each corner. None of the webs of the adult *A. argentata* that I have seen in southern South America had a complete stabilimentum; most lacked them completely. Juveniles have zigzag bands that are quite irregular (Plate I).

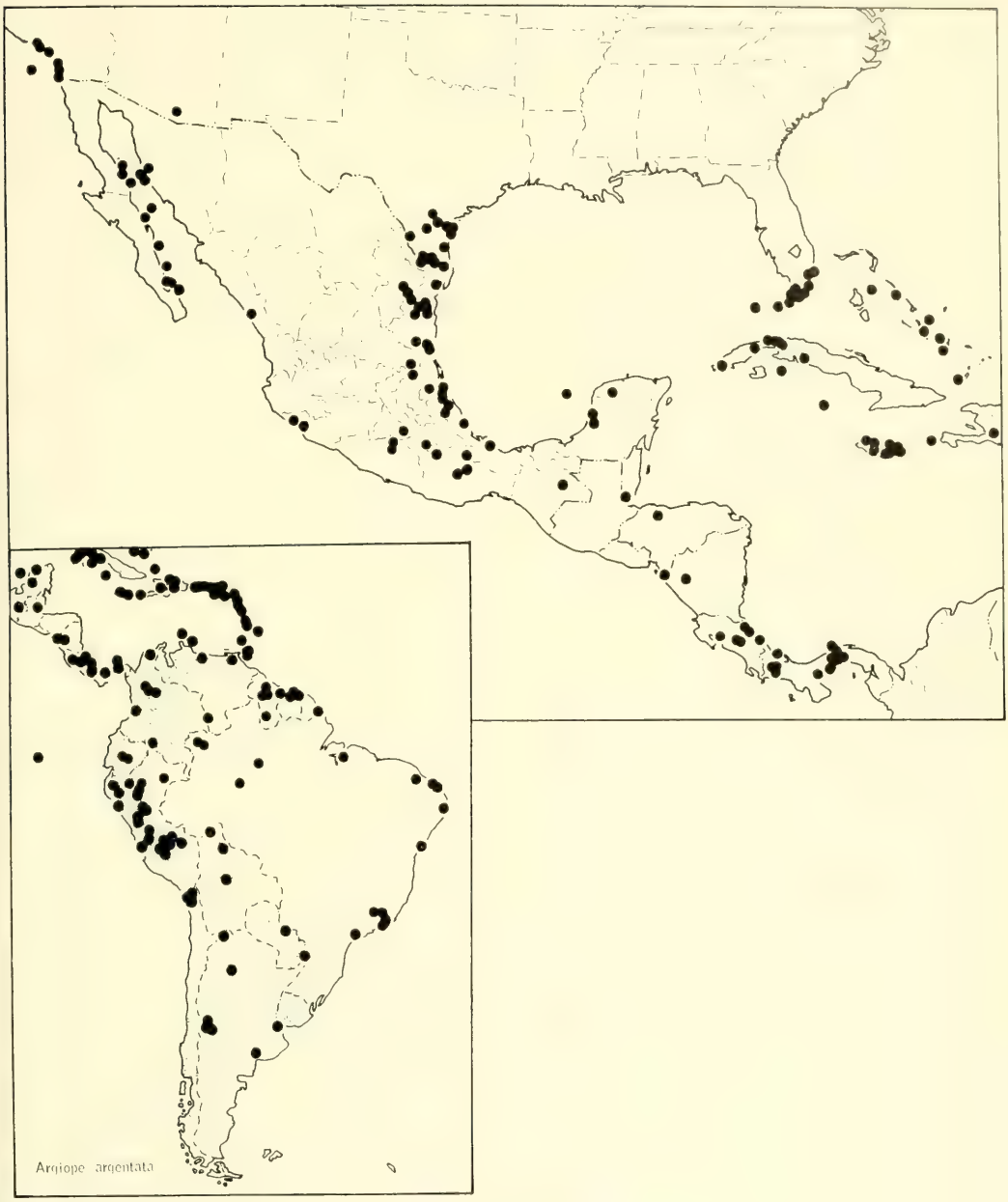
Distribution. Southern Arizona, probably southern California, southern Texas, southern Florida to Central Argentina, Provinces Mendoza and Buenos Aires. It is absent from Chile, except for the northernmost tip of the country (Map 5).

Argiope blanda O. P.-Cambridge
Mexican Argiope
Figures 137–153; Map 6

Argiope blanda O.P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, 1: 267, pl. 37, fig. 2, ♂. Male holotype from Santa Ana [20 km SW of Cobán] Guatemala, in the British Museum, not examined. F.P.-Cambridge, 1903, *ibid.*, 2, 451, pl. 43, fig. 1, ♂.

Description. Male. Carapace yellow-brown, some black pigment on each side. Sternum yellow-brown, black on each side, and a white pigment spot between last coxae. Legs with scattered black pigment. Dorsum of abdomen with white pigment and indistinct median darker foliate pattern (Fig. 148). Venter black with two longitudinal lines not very distinct, closer together, anteriorly. Anterior median eyes one diameter apart, about one radius from laterals. Posterior eyes about two diameters apart. Total length 3.4 mm. Carapace 1.7 mm long, 1.4 mm wide. First femur, 1.6 mm; patella and tibia, 2.1 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm; fourth, 1.6 mm.

Female. Carapace yellow-brown covered by white scales. Sternum black with a white spot between the 4th coxae (Fig. 144), legs indistinctly banded. Anterior half of dorsum of abdomen white, posterior mostly dark (Fig. 145). Venter black with a wide transverse white band. From the lateral ends of the white band, two median lines pass anteriorly towards the epigynum. Anterior median eyes one diameter apart, one and one-half diameters from laterals. Posterior median eyes almost two diam-



Map 5. Distribution of *Argiope argentata* (Fabricius).

eters apart, three diameters from laterals. The abdomen has posterior lateral tubercles and also a very distinct median dorsal tubercle (Figs. 145–147). Range of size of female 9–14 mm. Measurements of one specimen, total length 10 mm. Carapace 4.2 mm long, 3.2 mm wide. First femur, 5.9 mm; patella and tibia, 6.4 mm; metatarsus, 6.0 mm; tarsus, 1.8 mm. Second patella and tibia, 6.3 mm; third, 3.6 mm; fourth, 5.5 mm.

Diagnosis. The large thorn at the base of the embolus of the palpus is diagnostic (Figs. 149–151) and not found in other species. The epigynum of the female is very much like that of *A. argentata* but the posterior face of the epigynum (Fig. 142) is narrower, domed, and lacks depressions. To separate females, broken-off embolus tips usually found in the epigynum are useful.

Distribution. From southern Texas to Costa Rica (Map 6).

Argiope savignyi new species
Savigny's Argiope

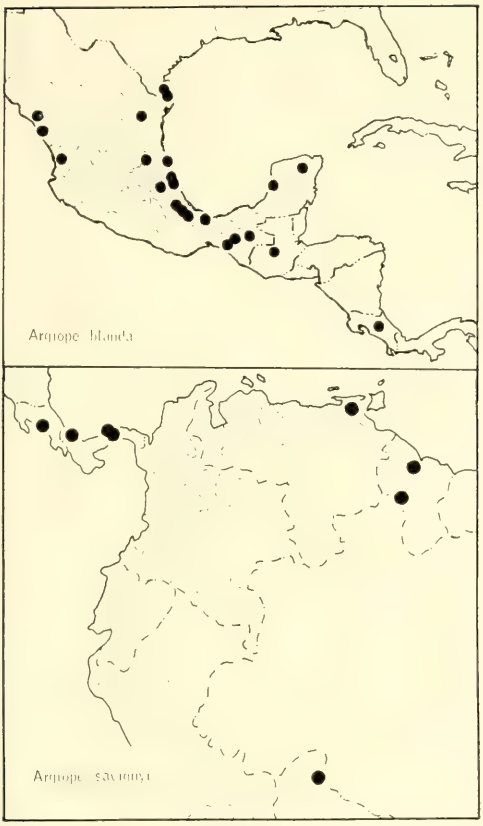
Figures 154–169; Map 6

Holotype. Male from Barro Colorado Island, Panama Canal Zone, 14–18 Jan. 1958, collected by A. M. Chickering, in the Museum of Comparative Zoology.

Description. Male. Area between eyes light. Eyes on black spots. Carapace otherwise dark bluish brown to black with a median light band which widens in the middle to wider than eye area and narrows anteriorly toward the posterior median eyes. Sternum light with a posterior narrow longitudinal white stripe and a black mark on each side anteriorly. Coxae and other leg segments dark bluish brown to black with proximal third of third femora and second tibiae and also metatarsi and tarsi light. Palpi light except cymbium, which is brown. Dorsum of abdomen with heavy white pigment. Venter of abdomen black with a bracket-shaped white mark on each side and a small white spot on each side of spinnerets. Anterior eye row straight as seen from front, posterior eye row procurved as seen from above. Ocular quadrangle longer than wide, wider behind. Anterior lateral eyes half the diameter of anterior medians, posterior median eyes twice the diameter of anterior medians, posterior lateral eyes 0.8 diameter of anterior medians. Anterior median eyes a little more than their diameter apart, same distance from laterals. Posterior median eyes one and one-half diameters apart, one and one-quarter diameters from laterals. Total length 3.4 mm. Carapace 2.1 mm long, 1.6 mm wide. First femur, 2.4 mm; patella and tibia, 2.4 mm; metatarsus, 2.1 mm; tarsus, 1.2 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.9 mm.

Female. Carapace brown, but covered with white, silky hairs. Sternum black with a wide, white median longitudinal band having some radiating white lines. Legs black. Dorsum of abdomen with heavy white pigment anteriorly and very few silvery hairs, posterior black (Fig. 161); venter black except for white marks shown in Figure 160. There is no continuous transverse white band on venter. Posterior eye row procurved, ocular quadrangle longer than wide, wider behind. Anterior lateral eyes smaller than others, the others about equal in size, lateral eyes on tubercles. Anterior median eyes one diameter apart, posterior median eyes one and one-half diameters apart. The abdomen is similar in shape to that of *Argiope argentata*, but the lateral tubercles seem more pointed. Total length 14 mm. Carapace 4.6 mm long, 4.2 mm wide. Measurements of first leg (which is broken off and might possibly be the second leg): femur, 8.4 mm; patella and tibia, 9.0 mm; metatarsus, 9.1 mm; tarsus, 2.1 mm. Third patella and tibia, 4.9 mm.

Diagnosis. The different color (Fig. 161), black where *Argiope argentata* is brown, the white dorsum of the abdomen with sparse, silvery hair and heavy pigment, and also the posterior swollen transverse section of the epigynum (Figs. 158, 159) separate the females readily from those of *A. argen-*



Map 6. Distribution of *Argiope blanda* O. P.-Cambridge and *A. savignyi* new species.

tata. The epigynum, like that of no related species, is filled with exudate after mating that clings to the broken-off embolus tip (Figs. 168, 169). The male differs from *A. argentata* also by the more contrasting colors and by lacking the fork at the tip of the embolus of the palpus (Figs. 166–169)[1].

Distribution. Costa Rica, British Guiana, to northern Bolivia (Map 6).

Records. Costa Rica, Puerto Viejo, Sarapiquí, 20 Jan. 1959, (S. M. Le Roi Léopold III, Brussels Museum). *Panama*. Bocas del Toro; Boquete 4–11 Aug. 1950, ♀ paratype (A. M. Chickering, Mus. Comp. Zool.); Gamboa, Aug.–Sept. 1954, ♀ paratype, (W. Lundy, Amer. Mus.); 4.8 km SW of Arraijan, Sept. 1945 (C. D. Michener, Amer. Mus.). *Panama Canal Zone*, Barro Colorado Isl. Old Plantation, 14 July 1954, ♀ paratype (A. M. Chickering, Mus. Comp. Zool.), Barro Colorado Island, July 1954, paratypes (Paris Museum), (A. M. Chickering), (N. Banks, Mus. Comp. Zool.), (H. F. Schwarz, Amer. Mus.), Gamboa, Aug.–Sept. 1954, ♀ paratype, (W. Lundy, Amer. Mus.), France Field, ♂ paratypes (A. M. Chickering). *Venezuela*: Caripito (W. Beebe, Amer. Mus.). *British Guiana*. Kartabo (Amer. Mus.); Kamakusa, Feb. 1923 (Lang, La Varce, Amer. Mus.). *Bolivia*. Cashuela Esperanza, Prov. Vaca Diez, ♀, 10–11 April 1922 (J. H. Williamson, Mus. Comp. Zool.).

[1] The stabilimentum of the *A. savignyi* web is in form of a cross. But as in *A. argentata* from Barro Colorado Island, it is rarely complete, sometimes a diagonal line, or just one or two bottom branches. The silk deposited on the stabilimenta may be more dense than that of *A. argentata* (M. H. Robinson, in letter, 1968).

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(Received 17 March 1967.)

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Bulletin OF THE
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Lichomolgid Copepods (Cyclopoida) Associated with Corals in Madagascar

ARTHUR G. HUMES AND JU-SHEY HO

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 10
APRIL 15, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

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Publications of the Boston Society of Natural History.

Publications Office
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LICHOMOLGID COPEPODS (CYCLOPOIDA) ASSOCIATED WITH CORALS IN MADAGASCAR

ARTHUR G. HUMES[1,2] AND JU-SHEY HO[1]

INTRODUCTION

Seven species of lichomolgid copepods are known to be associated with madreporarian corals in the region of Nosy Bé, Madagascar. These are *Lichomolgus actinophorus*, *Lichomolgus compositus*, and *Monomolgus unihastatus*, all described by Humes and Frost (1964); *Kombia angulata* Humes, 1962 (see below for a discussion of its familial position); and *Monomolgus psammocorae*, *Rhynchomolgus corallophilus*, and *Lichomolgus rhadinus*, all described by Humes and Ho (1967a). This paper deals with seven new species of *Lichomolgus* and three new lichomolgid genera, each with a single new species, collected from corals at Nosy Bé in 1960 and 1963–64.

All collections were made by A. G. Humes, those in 1960 during an expedition sponsored by the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition. Type material has been deposited in the United States National Museum. Other specimens of certain species have been placed in the Museum of Comparative Zoology.

The study of the specimens has been aided by grants (GB-1809 and GB-5838) from the National Science Foundation of the United States.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

The measurement of the length of the body has been made in all cases from specimens in lactic acid and does not include the setae on the caudal rami. In the spine and setal formulas of legs 1–4 the Roman numerals indicate spines and the Arabic numerals represent setae. The lengths of the segments of the first antenna have been measured along their posterior non-setiferous margins.

The abbreviations used are: A_1 = first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, MXPD = maxilliped, and P_1 = leg 1.

We are greatly indebted to Dr. Donald F. Squires of the United States National Museum for the identification of the corals collected in 1960, and to Dr. Michel Pichon, then at the Centre d'Océanographie et des Pèches at Nosy Bé, for the determinations of those collected in 1963–64.

The new copepods described in this paper comprise the following:

1) *Lichomolgus campulus* n. sp. from *Alveopora* sp.
2) *Lichomolgus digitatus* n. sp. from *Goniopora* sp.

[1] Boston University, Boston, Massachusetts.
[2] Associate in Marine Invertebrates, Museum of Comparative Zoology.

3) *Lichomolgus prolixipes* n. sp. from *Porites* sp. cf. *P. andrewsi* Vaughan, *Porites* sp. cf. *P. nigrescens* Dana, and *Porites* (s. g. *Synaraea*) sp.
4) *Lichomolgus arcuatipes* n. sp. from *Acropora palifera* (Lamarck)
5) *Lichomolgus lobophorus* n. sp. from *Acropora scherzeriana* Brueggemann, *Acropora* sp., and *Acropora cytherea* Dana
6) *Lichomolgus geminus* n. sp. from *Stylophora pistillata* (Esper), *Stylophora mordax* (Dana), and *Acropora* sp.
7) *Lichomolgus crassus* n. sp. from *Stylophora pistillata* (Esper), *Stylophora mordax* (Dana), and *Acropora* sp.
8) *Prionomolgus lanceolatus* n. gen., n. sp. from *Pachyseris speciosa* (Dana)
9) *Haplomolgus montiporae* n. gen., n. sp. from *Montipora sinensis* Bernard, *Montipora* sp., and *Montipora* sp. cf. *M. stellata* Bernard
10) *Ravahina tumida* n. gen., n. sp. from *Porites* sp. cf. *P. andrewsi* Vaughan

The following represent new host records:

1) *Lichomolgus actinophorus* Humes and Frost, 1964, from *Pavona danai* (M. Edwards and Haime), *Pavona* ? *venusta* (Dana), and *Pavona danai* or *P. angularis* (Klunzinger)
2) *Lichomolgus compositus* Humes and Frost, 1964, from *Seriatopora octoptera* Ehrenberg and *Seriatopora* sp.
3) *Monomolgus unihastatus* Humes and Frost, 1964, from *Porites* sp. cf. *P. nigrescens* Dana
4) *Kombia angulata* Humes, 1962, from *Porites* (s. g. *Synaraea*) sp., *Porites* (young colony), and *Porites* sp. cf. *P. nigrescens* Dana

SYSTEMATIC DESCRIPTION

LICHOMOLGIDAE Kossmann, 1877

LICHOMOLGUS Thorell, 1860

Lichomolgus campulus n. sp.

Figs. 1–24

Type material.—31 females, 32 males, and 2 copepodids from *Alveopora* sp. in a depth of 3.5 m, Nosy N'Tangam, on the western side of Nosy Bé, Madagascar. Collected October 23, 1964. Holotype female, allotype, and 50 paratypes (25 females and 25 males) deposited in the United States National Museum, Washington; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Fig. 1) moderately slender. Length 1.21 mm (1.15–1.26 mm) and greatest width 0.45 mm (0.43–0.47 mm), based on 10 specimens. Ratio of length to width of prosome 1.63:1. Epimeral areas of metasomal segments formed as in figure.

Segment of leg 5 (Fig. 2) 65×200 μ. Between this segment and genital segment a short weak ventral intersegmental sclerite. Genital segment broadened anteriorly and narrowed posteriorly, with slight lateral indentations, wider than long, its greatest dimensions being 180×224 μ. Areas of attachment of egg sacs located dorsally, each area (Fig. 3) with two small setae 6 and 10 μ long with a spinelike process between them. Three postgenital segments 86×107, 70×92, and 78×83 μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side.

Caudal ramus (Fig. 4) elongated, 105×33 μ, about 3.2 times longer than wide. Outer lateral seta 64 μ, outermost terminal seta 45 μ, innermost terminal seta 62 μ. Two long median terminal setae 260 μ (inner) and 150 μ (outer). Dorsal pedicellate seta 58 μ. All setae naked. Dorsal surface of ramus with a few minute hairs.

Dorsal surface of prosome and urosome with a few minute hairs as in Figure 1;

ventral surface of urosome almost entirely lacking ornamentation. Ratio of length of prosome to that of urosome 1.59:1.

Egg sac unknown.

Rostral area (Fig. 5) poorly developed, without a definite posteroventral margin.

First antenna (Fig. 6) slender, 370 μ long, and 7-segmented, with a sclerite on third segment suggesting an intercalary segment. Lengths of segments: 33 (78 μ along anterior margin), 133, 32, 43, 39, 28, and 19 μ, respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many other species of *Lichomolgus*. All setae naked.

Second antenna (Fig. 7) slender and 4-segmented. Penultimate segment 60 μ along outer edge, last segment 39 μ along outer edge and 20 μ along inner edge. Armature: 1, 1, 3, I. All setae small and naked; terminal claw 41 μ along its axis and rather sinuous.

Labrum (Fig. 8) with two posteroventral lobes.

Mandible (Fig. 9) with proximal region separated into two parts by a constriction. Region beyond constriction having on its convex side a row of small spinules and a prominent elongated posteriorly directed process; on its concave side two lobes each with a row of larger spinules. Flagellum elongated with lateral spinules. Paragnath (Fig. 10) a small lobe with a few hairs. First maxilla (Fig. 11) with three terminal elements, two of them broad and hyaline. Second maxilla (Fig. 12) 2-segmented. First segment large and unornamented. Second segment small, having proximally on its outer (ventral) margin a minute setule only 1.5 μ long followed by a naked seta and on its inner (dorsal) margin a barbed seta; terminal lash with a row of prominent spinules. Maxilliped (Fig. 13) moderately slender and 3-segmented; first segment unarmed, second with two very unequal inner naked setae, and third with a naked seta and a barbed seta, and terminating in a spiniform process with lateral spinules which bears a small setiform element on its outer surface.

Area between maxillipeds and first pair of legs (Fig. 5) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 14, 15, 16, and 17) with trimerous rami, except for endopod of leg 4 which is 2-segmented. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0–1; II

Inner seta on coxa of leg 4 somewhat smaller than in legs 1–3, with shorter lateral hairs. Hairs on inner margin of basis present in legs 1–3 but absent in leg 4. Endopod of leg 4 (Fig. 17) with hairs along outer margins of both segments. First segment 22 × 23 μ, its plumose inner seta 39 μ long. Second segment somewhat bottle-shaped, 35 × 20 μ in greatest dimensions, with two terminal unequal barbed spines 13 μ (outer) and 36 μ (inner) in length.

Leg 5 (Fig. 18) with an elongated free segment, 34 × 13 μ, without a basal expansion. Two terminal naked setae, outer 33 μ, inner 36 μ long. Seta on body near free segment 44 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 3).

Color in life in transmitted light slightly opaque, eye red.

Male.—Body (Fig. 19) moderately slender as in female. Length 1.11 mm (1.04–1.17 mm) and greatest width 0.39 mm (0.38–0.40 mm), based on 10 specimens. Ratio of length to width of prosome 1.40:1.

Segment of leg 5 (Fig. 20) 36 × 169 μ ventrally, 52 × 169 μ dorsally. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment rather quadrate in dorsal view, 208 × 242 μ, wider than long. Four postgenital seg-

ments 43 × 84, 46 × 80, 39 × 70, and 66 × 73 μ from anterior to posterior.

Caudal ramus resembling that of female, though smaller, 90 × 28 μ.

Dorsal and ventral surfaces of body ornamented with a few minute hairs as in female. Ratio of length of prosome to that of urosome 1.20:1.

Rostral area like that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4 (their positions indicated by small arrows in Figure 6), so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All aesthetes a little longer than in female. Second antenna (Fig. 21) resembling that of female, but inner surface of second segment with short spinelike bosses; third segment with a few similar bosses and with three elements, two hyaline and obtuse, the other setiform.

Labrum, mandible, paragnath, first maxilla, and second maxilla resembling those in female. Maxilliped (Fig. 22) slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. First segment unarmed, second with two setae and two rows of spinules on inner surface, third small and unarmed. Claw only slightly recurved, 151 μ along its axis (including terminal lamella), with faint indication of division midway; proximally with two unequal naked setae, distal half of longer one hyaline and blunt.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female.

Leg 5 (Fig. 23) with a short free segment, 15 × 9 μ, its terminal setae being 24 and 33 μ in length.

Leg 6 (Fig. 24) consisting of a posteroventral flap on genital segment, bearing two small naked setae about 20 μ long.

Spermatophore not observed.

Color in life in transmitted light similar to female.

Etymology.—The specific name *campulus*, from καμπύλος = bent, refers to the sinuous nature of the claw on the second antenna.

Comparison with related species.—The presence of a prominent elongated process on the basal part of the mandible distinguishes this species from most other species of *Lichomolgus*. Only six other species (among the seventy or more described in the genus) have a process which is at all comparable. *L. actinophorus* Humes and Frost, 1964, has an elongated posteriorly directed process on the mandible, but this process is more pointed and dentiform than in the new species. Furthermore, *L. actinophorus* has a setiferous spherical process on the second maxilla, distinguishing it from *L. campulus*. *L. decorus* Humes and Frost, 1964, has an anteriorly directed toothlike process on the mandible and the formula for the last segment of the exopod of leg 4 is III, I, 5. In *L. organicus* Humes and Ho, 1967b, and *L. conjunctus* Humes and Ho, 1967b, there is a posteriorly directed toothlike process on the mandible, the caudal ramus is not more than 1.5 times longer than wide, and there are two claws on the second antenna. *L. protulae* Stock, 1959, has an anteriorly directed tooth on the mandible, greatly elongated caudal rami, and several claws on the second antenna. *L. rhadinus* Humes and Ho, 1967a, has a process on the mandible rather similar to that in *L. campulus*, but the two species may readily be distinguished. The female of *L. rhadinus* has an inner basal expansion on the elongated (about 5:1) free segment of leg 5 and the genital segment is rather abruptly indented posteriorly on both sides in dorsal view. The male of *L. rhadinus* has a much shorter caudal ramus (28 × 18 μ), its leg 1 shows sexual dimorphism (the last segment being I, I, 4 instead of I, 5 as in the female), and the genital segment is longer than wide. In spite of these clear differences, *L. campulus* seems to be more closely related to *L. rhadinus* than to any other species.

There are eight species of *Lichomolgus*

in which the form of the mandible, being unknown, can not be compared with that of the new species. (Thompson and A. Scott, 1903, did not describe the mandible of their *Lichomolgus gigas*, but stated, p. 280, that the "mouth organs . . . nearly resemble *L. simplex*.") All eight, however, possess characters which distinguish them from *L. campulus*. Thus, *L. dentipes* Thompson and A. Scott, 1903, and *L. rigidus* (Ummerkutty, 1962) have the formula for the last segment of the exopod of leg 4 as III, I, 5; *L. gigas* Thompson and A. Scott, 1903, is much larger (female 2 mm, male 1.4 mm); *L. longipes* (Sewell, 1949), *L. rotundus* Sewell, 1949, *L. tenuicornis* Brady, 1910, and *L. vagans* Gurney, 1927, have two claws on the last segment of the second antenna; and *L. elegans* Thompson and A. Scott, 1903, has the caudal ramus about as broad as long.

Lichomolgus digitatus n. sp.

Figs. 25–52

Type material.—9 females, 4 males, and 2 immature specimens from *Goniopora* sp. in a depth of 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected April 10, 1964. Holotype female, allotype, and 9 paratypes (7 females and 2 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Fig. 25) with prosome moderately broadened. Length 1.89 mm (1.73–2.00 mm) and greatest width 0.70 mm (0.66–0.73 mm), based on 9 specimens. Ratio of length to width of prosome 1.49:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 26) 83 × 255 μ. Between this segment and genital segment a weak ventral intersegmental sclerite. Genital segment broadened anteriorly and tapered posteriorly, wider than long, 253 × 290 μ in greatest dimensions. Areas of attachment of egg sacs located dorsally, each area (Fig. 27) with two small setae (7 and 10 μ long) and a small spinelike process. Three postgenital segments 82 × 122, 55 × 107, and 101 × 104 μ from anterior to posterior. Spinules on posteroventral margin of anal segment very few in number and minute.

Caudal ramus (Fig. 28) elongated, 220 × 36 μ, about 6.1 times longer than wide. Setae relatively short and naked. Outer lateral seta 33 μ, outermost terminal seta 28 μ, innermost terminal seta 33 μ. Two long median terminal setae 172 μ (inner) and 133 μ (outer). Dorsal pedicellate seta very short, 14 μ. Dorsal surface of ramus with refractile points. A minute spinule 5 μ long on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with scattered refractile points and small hairs as in Figure 25. Ratio of length of prosome to that of urosome 1.37:1.

Egg sac unknown.

Rostral area (Fig. 29) weakly developed.

First antenna (Fig. 30) slender, 390 μ long, segmented and armed as in the previous species. Lengths of segments: 40 (68 μ along anterior margin), 120, 28, 55, 57, 39, and 24 μ respectively. All setae naked.

Second antenna (Fig. 31) 4-segmented, with two proximal segments stouter than in *L. campulus*. Penultimate segment 66 μ along outer edge, last segment 44 μ along outer edge and 31 μ along inner edge. A sclerotized bar running diagonally across outer surface of last segment. Armature: 1, 1, 3, I + 3 minute setules. All setae small and naked; terminal claw 29 μ along its axis and not recurved.

Labrum (Fig. 32) with two posteroventral lobes.

Mandible (Fig. 33) more massive than in *L. campulus*, with a less prominent constriction in proximal region. On convex side a short row of spinules (apparently not always present) and two unequal digitiform hyaline processes, followed by a long row of spinules. Concave margin beyond constriction with two prominent lobes armed with spinules. Flagellum

elongated with lateral spinules. Paragnath (Fig. 34) a small lobe with hairs. First maxilla (Fig. 35) with four lamellate elements and a patch of minute spinules. Second maxilla (Fig. 36) 2-segmented, first segment large and unornamented. Second segment with a small setuliform process on its proximal outer (ventral) margin, a lamellate seta on its anterior surface, and a seta with a striated membranous lamella on its inner (dorsal) margin; terminal lash with a row of spinules. Maxilliped (Fig. 37) stout and 3-segmented; first segment unarmed; second with two naked inner setae and an outer patch of spinules; and third with a slender seta, a spine, and a terminal spiniform process, all naked.

Area between maxillipeds and first pair of legs (Fig. 38) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 39, 40, 41, and 42) segmented as in the previous species, with same spine and setal formula. Leg 4 with inner seta on coxa naked and 31 μ long; hairs present on inner margin of basis. Endopod of leg 4 with hairs along inner margins of both segments. First segment 34×30 μ, its plumose inner seta 73 μ long. Second segment 70×28 μ in greatest dimensions, with its two terminal unequal fringed spines 37 μ (outer) and 74 μ (inner) in length.

Leg 5 (Fig. 43) with a moderately elongated free segment, 36×17 μ in greatest dimensions, without a basal expansion. Two unequal naked terminal setae 20 and 39 μ. Seta on body near free segment 36 μ. All setae naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 27).

Color in life in transmitted light translucid, eye dark red.

Male.—Body (Fig. 44) with prosome moderately broadened as in female. Length 1.55 mm (1.48–1.62 mm) and greatest width 0.54 mm (0.52–0.59 mm), based on 4 specimens. Ratio of length to width of prosome 1.38:1.

Segment of leg 5 (Fig. 45) 52×177 μ ventrally, 60×177 μ dorsally. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment subquadrate in dorsal view, 275×290 μ, a little wider than long. Four postgenital segments 52×91, 55×90, 39×83, and 79×83 μ from anterior to posterior.

Caudal ramus resembling that of female, but shorter, 166×39 μ, about 4.3 times longer than wide.

Dorsal and ventral surfaces of body ornamented with scattered refractile points and small hairs (Fig. 44) as in female. Ratio of length of prosome to that of urosome 1.06:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is same as for male of *L. campulus*. Second antenna (Fig. 46) resembling that of female, but inner surface of second segment with sclerotized spinelike knobs.

Labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. (Mandibles in single male dissected lacking short row of spinules near digitiform processes.) Maxilliped (Fig. 47) slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. First segment unarmed, second with two barbed setae and a row of spinules on inner surface, third small and unarmed. Claw recurved, 270 μ along its axis (including terminal lamella), with slight evidence of division midway; proximally with two very unequal setae, the longer one bent and having fine lateral spinules in its distal half.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female, except for sexual dimorphism on last segment of endopod of leg 1 (Fig. 48), where formula is I, I, 4, instead of I, 5 as in female.

Leg 5 (Fig. 49) with free segment more slender than in female, 31×9 μ, its two terminal naked setae 27 and 40 μ in length.

Leg 6 (Fig. 50) a posteroventral flap on

genital segment, bearing two small naked setae about 23 μ long.

Spermatophore not observed.

Color in life as in female.

Etymology.—The specific name *digitatus*, from Latin = having fingers, alludes to the small fingerlike processes on the mandible.

Notes on copepods from Porites, closely resembling L. digitatus.—Six females and five males which differ slightly from *L. digitatus* in the proportions of certain parts were recovered from a piece of a massive colony of *Porites* sp. in 1 m, at Ampora, Nosy Bé, October 22, 1964.

One female measures 1.94×0.72 mm. The genital segment is slightly larger, 275×352 μ. The caudal ramus (Fig. 51) is relatively a little longer, 286×42 μ, or 6.8 times longer than wide. The endopod of leg 4 (Fig. 52) is longer, the first segment 50×34 μ with its inner seta 110 μ, the second segment 92×25 μ with its two terminal spines 44 and 94 μ. The free segment of leg 5 is a little longer, 46×19 μ.

One male measures 1.76×0.60 mm. The genital segment is larger and slightly wider, 341×400 μ. The caudal ramus is relatively longer, 247×39 μ, or 6.33 times longer than wide. The claw on the maxilliped is relatively longer, 335 μ. The second segment of the endopod of leg 4 is 88×28 μ. The free segment of leg 5 is 44×14 μ.

In other respects, such as details of the armature and ornamentation, these copepods from *Porites* are identical with *L. digitatus*. The differences mentioned above, concerning chiefly proportions and based on very few specimens, probably should not be considered at present to be of specific or even subspecific rank. Perhaps the future study of a large series of these copepods from both *Porites* and *Goniopora* would clarify the significance of such proportional differences.

Comparison with related species.—There are fifteen species already described in the genus *Lichomolgus* which have the combination of one claw (often with other small elements) on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4, thus resembling the new species. These are: *L. actinophorus* Humes and Frost, 1964, *L. anomalus* A. Scott, 1909, *L. arcanus* Humes and Cressey, 1958, *L. asaphidis* Humes, 1959, *L. campulus*, *L. chamarum* Humes, in press, *L. compositus* Humes and Frost, 1964, *L. elongatus* Buchholz, 1869, *L. gigas* Thompson and A. Scott, 1903, *L. inflatus* Tanaka, 1961, *L. politus* Humes and Ho, 1967*d*, *L. rhadinus* Humes and Ho, 1967a, *L. simulans* Humes and Ho, 1967*d*, *L. spondyli* Yamaguti, 1936, and *L. trochi* Canu, 1899. In only one of these, *L. gigas*, does the mandible resemble that of *L. digitatus* in apparently having two small digitiform processes on the convex side. (Although Thompson and A. Scott did not describe the mouthparts of *L. gigas* in detail, they stated, p. 280, that they nearly resemble those of *L. simplex*, in which the mandible has two "small corner filaments," illustrated on their pl. XV, fig. 30). However, the shape of the genital segment in the female, the relative size of leg 5 in the female, and the relative sizes of segments 3 and 4 of the second antenna (the fourth much longer than the third) distinguish this Ceylonese species from *L. digitatus*.

L. elegans Thompson and A. Scott, 1903, of which only the female is known, has only one claw on the second antenna, but the formula for the last segment of the exopod of leg 4 is unknown. However, this species may be easily distinguished from the new species by its very short caudal ramus, which is about as broad as long, and by the notched genital segment.

Lichomologus prolixipes n. sp.

Figs. 53–78

Type material.—4 females and 3 males from *Porites* sp. cf. *P. andrewsi* Vaughan in a depth of 3 m, Pte. de Tafondro, Nosy Bé, Madagascar. Collected September 28, 1960. (This is the same colony of coral from which the types of *Monomolgus unihastatus* Humes and Frost, 1964, were col-

lected.) Holotype female, allotype, and 2 paratypes (one female and one male) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens.—From *Porites* sp. cf. *P. andrewsi*: 4 females in 0.5 m, at the point north of the village of Madirokely, Nosy Bé, October 24, 1960. From *Porites* sp. cf. *P. nigrescens* Dana: 2 females in 1 m, Pte. de Tafondro, Nosy Bé, September 19, 1963. From *Porites* (s. g. *Synaraea*) sp.: 3 females in 1 m, Pte. Lokobe, Nosy Bé, November 20, 1963; 4 females and 2 males in 1–2 m, Ankify, on the mainland of Madagascar, near Nosy Bé, December 30, 1963.

Female.—Body (Fig. 53) with rather slender prosome, cephalosome somewhat pointed anteriorly. Length 1.11 mm (1.05–1.15 mm) and greatest width 0.47 mm (0.46–0.47 mm), based on 4 specimens. Ratio of length to width of prosome 1.41:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 54) 58 × 156 μ. Between this segment and genital segment a very weakly developed ventral intersegmental sclerite. Genital segment 177 μ in length, broadened in its anterior two-thirds (156 μ wide) but constricted in its posterior third (88 μ wide). Areas of attachment of egg sacs situated dorsally, each area (Fig. 55) with two small setae (anterior seta held erect and not measured, posterior seta 17 μ in length) and a small spinous process. Three postgenital segments 49 × 75, 43 × 72, and 69 × 72 μ from anterior to posterior. A row of minute spinules on posteroventral margin of anal segment.

Caudal ramus (Fig. 57) moderately elongated, 77 × 29 μ, 2.65 times longer than wide. Setae longer than in preceding species and naked except for the two long setae. Outer lateral seta 85 μ, outermost terminal seta 117 μ, innermost terminal seta 112 μ. Two long median terminal setae 390 μ (inner) and 275 μ (outer), with their edges in midregion roughened to suggest presence of extremely short lateral barbules, but these not clearly visible under oil immersion. Dorsal pedicellate seta relatively short, 50 μ. Dorsal surface of ramus with a few small hairs. No spinule seen on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with few scattered hairs and refractile points as in Figures 53 and 54. Ratio of length of prosome to that of urosome 1.57:1.

Egg sac (Fig. 57) relatively small, 385 × 220 μ in lateral view, containing about nine eggs, each approximately 112 μ in diameter.

Rostral area (Fig. 58) weakly developed.

First antenna (Fig. 59) slender, 341 μ long, segmented and armed as in previous two species. Lengths of segments: 28 (50 μ along anterior margin), 113, 28, 62, 40, 30, and 18 μ, respectively. All setae naked.

Second antenna (Fig. 60) 4-segmented, more slender than in *L. digitatus*. Penultimate segment 40 μ along outer edge, last segment 37 μ along outer edge and 21 μ along inner edge. Armature: 1, 1, 3, I. Setae small and naked. Apparently no setules near base of terminal claw, which is recurved and 42 μ along its axis.

Labrum (Fig. 61) with two posteroventral lobes of somewhat irregular outline and with hyaline medial margins.

Mandible (Fig. 62) resembling that of *L. digitatus*, with two similar digitiform processes on convex edge, but without spinules near the processes and with flagellum a little shorter. Paragnath (Fig. 63) a small lobe with hairs. First maxilla (Fig. 64) with three terminal elements and a lateral fringe. Second maxilla (Fig. 65) resembling that of *L. digitatus*, but second segment with process on proximal outer (ventral) margin broad and hyaline and seta on inner (dorsal) margin with hyaline lamellae. Maxilliped (Fig. 66) 3-segmented; first segment unarmed; second with two very unequal naked setae and lacking outer patch of spinules seen in previous species; third with two unequal naked setae and

a short terminal finely barbed spiniform process.

Area between maxillipeds and first pair of legs (Fig. 58) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 67, 68, 69, and 70) segmented as in previous two species, with same spine and setal formula. Leg 4 with inner seta on coxa minute and naked, 5 μ long; hairs present on inner margin of basis. Endopod of leg 4 with hairs along outer margins of both segments. First segment 26 × 20 μ in greatest dimensions, its plumose inner seta relatively short, 30 μ. Second segment 44 × 18 μ, with its two terminal fringed spines 31 μ (outer) and 41 μ (inner) in length.

Leg 5 (Fig. 71) with slightly recurved free segment greatly elongated, 203 × 30 μ, or 6.76 times longer than wide, reaching a little beyond posterior end of genital segment. Very small spinules along outer surface. Two naked terminal setae 80 μ (outer) and 100 μ (inner) in length; seta on body near free segment 65 μ long (a row of minute spinules near insertion of this seta).

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 55).

Color in life in transmitted light translucid to opaque, eye red.

Male.—Body (Fig. 72) with prosome more slender than in female, cephalosome more rounded anteriorly. Length 0.82 mm (0.80–0.85 mm) and greatest width 0.30 mm (0.28–0.31 mm), based on 3 specimens. Ratio of length to width of prosome 1.65:1.

Segment of leg 5 (Fig. 73) 39 × 90 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment longer than wide, 165 × 138 μ. Four postgenital segments 24 × 56, 26 × 53, 19 × 51, and 33 × 53 μ from anterior to posterior.

Caudal ramus resembling that of female, but shorter, 46 × 23 μ, or 2 times longer than wide.

Dorsal and ventral surfaces of body ornamented as in female with a few hairs and refractile points (Figs. 72 and 73). Ratio of length of prosome to that of urosome 1.43:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 72), so that formula is same as for males of previous two species. Second antenna (Fig. 74) resembling that of female, but having small spinelike knobs along inner surface of second segment.

Labrum, mandible, paragnath, first maxilla, and second maxilla similar to those in female. Maxilliped (Fig. 75) slender, segmented and armed as in *L. digitatus*; spinules on inner surface of second segment longer than in that species, and claw 172 μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female, except for leg 1 which shows sexual dimorphism in last segment of endopod, formula here being I, I, 4 (Fig. 76), instead of I, 5 as in female.

Leg 5 (Fig. 77) with free segment much shorter than in female, 35 × 10 μ, its two terminal setae 60 μ (outer) and 68 μ (inner), and seta on body adjacent to free segment 58 μ. All setae naked as in female.

Leg 6 (Fig. 78) a posteroventral flap on genital segment, bearing two small naked setae 41 μ and 28 μ in length.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *prolixipes*, from Latin *prolixus* = long, and *pes* = foot, refers to the unusually long fifth legs in the female.

Comparison with related species.—*L. prolixipes* and *L. digitatus* show several features in common which indicate their close relationship. In both, the mandible has similar digitiform processes, the second antenna has a single claw, the formula for the last segment of the exopod of leg 4 is II, I, 5, and there is similar sexual dimor-

phism in the last segment of the endopod of leg 1 (female I, 5, male I, I, 4).

The new species may be readily distinguished from *L. digitatus*, however, by its smaller size, its shorter caudal rami, the shape of the genital segment, and the form of leg 5.

The distinctions made above in comparing *L. digitatus* with other species of *Lichomolgus* (which have the combination of one claw on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4) apply also to *L. prolixipes*.

Lichomologus arcuatipes n. sp.

Figs. 79–104

Type material.—137 females, 111 males, and 13 immature specimens from *Acropora palifera* (Lamarck) in a depth of 2 m, Tany Kely, a small island to the south of Nosy Bé, Madagascar. Collected August 22, 1963. Holotype female, allotype, and 90 paratypes (50 females and 40 males) deposited in the United States National Museum, the same number of paratypes in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Acropora palifera*).—84 females, 32 males, and 9 immature specimens in 2 m, Tany Kely, October 3, 1963; 61 females, 39 males, and 1 immature specimen in 0.5 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, June 21, 1963.

Female.—Body (Fig. 79) with rather broadened prosome. Length 1.06 mm (1.01–1.11 mm) and greatest width 0.40 mm (0.38–0.41 mm), based on 10 specimens. Ratio of length to width of prosome 1.34:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 80) 57 × 208 μ. Between this segment and genital segment no clearly defined ventral intersegmental sclerite. Genital segment subquadrate, 133 × 159 μ, a little wider than long, in dorsal view broadest in its anterior fourth and tapering slightly posteriorly. Areas of attachment of egg sacs located dorsally, each area (Fig. 81) with two small setae about 6 μ long. Three postgenital segments 75 × 89, 66 × 58, and 62 × 48 μ from anterior to posterior. A row of minute spinules along posteroventral border of anal segment.

Caudal ramus (Fig. 82) elongated, 130 × 18 μ, 7.2 times longer than wide. Certain setae with lateral spinules as in figure. Outer lateral seta 60 μ, outermost terminal seta 64 μ, innermost terminal seta 86 μ. Two long median terminal setae 180 μ (inner) and 117 μ (outer). Dorsal pedicellate seta 75 μ. Dorsal surface of ramus with a few small hairs, ventral surface with sclerotized knobs. No spinule seen on proximal outer margin of ramus.

Dorsal surfaces of prosome and urosome with scattered hairs and refractile points, ventral surface of urosome with refractile knobs (as on this surface of caudal ramus). Ratio of length of prosome to that of urosome 1.30:1.

Egg sac (Fig. 79) small, globular, 198 × 187 μ in dorsal view, containing usually 3 eggs (sometimes only 2) flattened against each other.

Rostral area (Fig. 83) not well developed, with refractile knobs.

First antenna (Fig. 84) slender, 278 μ long, segmented and armed as in previous three species. Lengths of segments: 21 (44 μ along anterior edge), 83, 23, 50, 39, 22, and 17 μ, respectively. All setae naked. A group of surficial sclerotizations on proximal dorsal surface of second segment.

Second antenna (Fig. 85) 3-segmented, last two segments being fused, with only a slight break in sclerotization of outer wall indicating bipartite nature. Armature: 1, 1, 2 + I. Last segment (fusion of original segments 3 and 4) with two minute spiniform projections, perhaps representing remnants of two of the three setae often present here in *Lichomolgus*. Terminal claw straight, about 20 μ long, apparently lacking an actual articulation with segment, no small elements near base of claw. With

scalelike knobs on antero-outer surface of second segment.

Labrum (Fig. 86) similar in general form to that of the previous species.

Mandible (Fig. 87) resembling that of *L. digitatus*, but distal convex margin produced, forming two lobes, proximal one with four slender digitiform processes, distal one broadly triangular. Paragnath (Fig. 88) a small lobe with hairs. First maxilla (Fig. 89) with three terminal elements. Second maxilla (Fig. 90) resembling that of the previous species, but element on proximal outer (ventral) margin a slender setule. Maxilliped (Fig. 91) slender, 3-segmented; first segment unarmed; second with two very unequal naked setae; third with two small naked elements and a short barbed terminal spiniform process.

Area between maxillipeds and first pair of legs (Fig. 92) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 93, 94, 95, and 96) segmented as in previous three species, with same spine and setal formula. Outer spines of exopods with either smooth or serrate lamellae, those of leg 1 as in Figure 93, those of legs 2 and 3 as in Figure 94, and those of leg 4 as in Figure 95. Leg 4 with inner coxal seta short, 16 μ, with a few lateral hairs proximally; hairs present on inner margin of basis. Endopod of leg 4 with hairs along outer margins of both segments and along inner distal margin of second segment. First segment 29×22 μ, with plumose inner seta 40 μ. Second segment 58×20 μ (greatest dimensions) with its two terminal fringed spines 39 μ (outer) and 47 μ (inner) in length.

Leg 5 (Fig. 97) with free segment elongated and strongly arched, with its tip extending dorsally over genital segment (as in Figure 80); dimensions about 117×24 μ, with inner surface slightly concave and outer surface convex and ornamented with short broad spinules. Two terminal naked setae 28 μ (outer) and 87 μ (inner). Naked seta on body near free segment 83 μ. A row of spinules on body near insertion of free segment.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 81).

Color in life in transmitted light translucid to opaque, eye red, egg sacs gray.

Male.—Body (Fig. 98) with rather broadened prosome as in female. Length 1.23 mm (1.15–1.28 mm) and greatest width 0.40 mm (0.39–0.43 mm), based on 10 specimens. Ratio of length to width of prosome 1.42:1.

Segment of leg 5 (Fig. 99) 55×153 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment quadrate, 208×200 μ. Four postgenital segments 65×81, 68×70, 62×60, and 78×60 μ, from anterior to posterior.

Caudal ramus resembling that of female, but larger in absolute dimensions, 161×24 μ, ratio of length to width a little less, 6.7:1.

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 0.88:1, urosome being a little longer than prosome.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 98), so that formula is same as for males of previous three species. Second segment with surficial sclerotizations as in female. Second antenna (Fig. 100) resembling that of female, but with inner margin of second segment somewhat irregular with two protuberances bearing scalelike knobs. Claw a little shorter and stouter than in female.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 101) slender, segmented and armed as in the previous species; prominent spinules in two rows on inner surface of second segment. Claw 234 μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling those in female, with similar segmentation and with same spine and setal formula, except for last segment of endopod of leg 1 (Fig. 102) where armature is I, I, 4, instead of I, 5 as in female. Outer spines (except first and last) on exopod of leg 2 showing finely serrated proximal lamellae (instead of smooth as in female); outer terminal spine on endopod of this leg with its outer lamella serrated instead of smooth.

Leg 5 (Fig. 103) with elongated straight free segment, 48 × 12 μ, without surficial ornamentation and much smaller than in female. Two terminal setae 34 μ (outer) and 13 μ (inner), and seta on body near free segment 60 μ. All setae naked.

Leg 6 (Fig. 104) a posteroventral flap on genital segment, bearing two small naked setae 17 and 23 μ in length.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *arcuatipes*, from Latin *arcuatus* = bent in the form of a bow, arched, and *pes* = foot, refers to the form of the fifth legs in the female.

Comparison with related species.—From those species of *Lichomolgus* having one claw on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4 (see list above under *L. digitatus*), *L. arcuatipes* may be distinguished by the two lobes on the convex margin of the mandible, one with four slender digitiform processes, the other broadly triangular. These features are not present in any of the fifteen species listed above or in either *L. digitatus* or *L. prolixipes*.

Only one other species of *Lichomolgus*, *L. compositus* Humes and Frost, 1964, has a 3-segmented second antenna, but this species is unlike *L. arcuatipes* in such features as the number of eggs in the egg sac, the nature of the setae on the caudal rami, the surficial ornamentation of the second segment of the first antenna, the armature of the second maxilla, the nature of the outer spines on the exopods of legs 1–4, and the form and ornamentation of leg 5.

L. elegans Thompson and A. Scott, 1903, has one claw on the second antenna, but the formula for the last segment of the exopod of leg 4 is unknown. This species, however, has a very short caudal ramus, about as broad as long, and an elongated notched genital segment, thus distinguishing it from *L. arcuatipes*.

Lichomolgus lobophorus n. sp.

Figs. 105–133

Type material.—21 females, 15 males, and 2 immature specimens from *Acropora scherzeriana* Brueggemann in a depth of 1 m, Pte. Lokobe, Nosy Bé, Madagascar. Collected October 25, 1960. Holotype female, allotype, and 30 paratypes (18 females and 12 males) deposited in the United States National Museum, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Acropora* sp.: 12 females and 20 males in 1 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, September 17, 1963; 27 females, 19 males, and 1 immature specimen in 0.5 m, Ambariobe, October 20, 1963. From *Acropora cytherea* Dana: 14 females and 6 males in 1 m, Andilana (sometimes spelled Andilah), Nosy Bé, September 4, 1960.

Female.—Body (Fig. 105) with moderately broadened prosome. Length 1.27 mm (1.21–1.36 mm) and greatest width 0.50 mm (0.47–0.52 mm), based on 10 specimens. Ratio of length to width of prosome 1.44:1. Epimeral areas of metasomal segments expanded as in figure.

Segment of leg 5 (Fig. 106) 104 × 280 μ. Between this segment and genital segment a faint indication of an intersegmental sclerite ventrally. Genital segment rectangular, a little longer than wide, its lateral margins slightly indented in dorsal view. Length 247 μ, width in anterior half 234 μ and in posterior half 228 μ. Areas of attachment of egg sacs situated dorsally, each area

(Fig. 107) with two small naked setae about 7 μ long separated by a minute spinous process; adjacent area with hyaline setules. Three postgenital segments (Fig. 108) 120×164, 70×107, and 114×91 μ, measured dorsally, from anterior to posterior. First postgenital segment asymmetrical in lateral view (Fig. 109), extended ventrally and posteriorly as a prominent broad lobe underlying part of next segment (cf. Figure 108); ventral length of segment including lobe 169 μ. A row of minute spinules along outer posterior border of anal segment.

Caudal ramus (Fig. 110) elongated, 180×29 μ, 6.2 times longer than wide. Certain setae with lateral spinules as in figure. Outer lateral seta 73 μ, outermost terminal seta 65 μ, innermost terminal seta 73 μ. Two long median terminal setae 95 μ (inner) and 83 μ (outer). Dorsal pedicellate seta 55 μ. Dorsal and ventral surfaces of ramus with hairs and refractile areas (which appear to be minute depressions in the cuticula rather than knobs). No spinule seen on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with a few hairs and numerous refractile areas (apparently slight depressions in the cuticula). Ratio of length of prosome to that of urosome 1.42:1.

Egg sac (Figs. 105 and 111) small, globular, 237×195 μ in dorsal view, containing 6–7 eggs of somewhat irregular shape.

Rostral area (Fig. 112) not well developed, but covered anteriorly with refractile points.

First antenna (Fig. 113) slender, 376 μ long, segmented and armed as in previous four species. Lengths of segments: 31 (55μ along anterior edge), 136, 28, 62, 46, 28, and 21 μ, respectively. All setae naked.

Second antenna (Fig. 114) 3-segmented, last two segments having been fused, as in *L. arcuatipes*, but fusion even more complete, without an interruption in sclerotization of outer wall and without a trace of three setae usually seen on penultimate segment in *Lichomolgus*. Armature: 1, 1 (very small), I. Terminal claw straight, about 20 μ long, without definite articulation with segment; no minute elements near base of claw. Antero-outer surface of second segment with refractile areas (which, like those on body surface, seem to be slight depressions in the cuticula rather than knobs).

Labrum (Fig. 115) with two lobes more pointed than in previous species.

Mandible (Fig. 116) closely resembling that of *L. arcuatipes*. Paragnath (Fig. 117) a small hairy lobe. First maxilla (Fig. 118) with three terminal elements. Second maxilla (Fig. 119) and maxilliped (Fig. 120) much like those of *L. arcuatipes*.

Area between maxillipeds and first pair of legs (Fig. 121) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 122, 123, 124, and 125) segmented as in previous four species, with same spine and setal formula. Inner coxal seta of leg 4 moderately long, 41 μ, and haired; basis of this leg with hairs on inner margin. Endopod of leg 4 resembling that of *L. arcuatipes*. First segment 36×30 μ, with its plumose inner seta 69 μ. Second segment attenuated distally, 81×28 μ (greatest dimensions), with its two terminal fringed spines 50 μ (outer) and 57 μ (inner) in length.

Leg 5 (Fig. 126) with free segment elongated and arched (but less strongly so than in the previous species), dimensions about 200×35 μ, with outer convex surface ornamented with short stout spinules. Two terminal naked setae 38 μ (outer) and 75 μ (inner). Naked seta on body near free segment 90 μ. A row of spinules on body near insertion of free segment.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 107).

Color in life in transmitted light slightly amber, eye red, egg sacs gray.

Male.—Body (Fig. 127) with moderately broadened prosome. Length 1.15 mm

(1.11–1.19 mm) and greatest width 0.39 mm (0.37–0.39 mm), based on 10 specimens. Ratio of length to width of prosome 1.40:1.

Segment of leg 5 (Fig. 128) 65 × 166 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment quadrate, 260 × 270 μ, only a little wider than long. Four postgenital segments 78 × 112, 65 × 81, 50 × 72, and 90 × 71 μ, measured dorsally, from anterior to posterior. Second postgenital segment with a prominent broad posteroventral lobe as in female.

Caudal ramus resembling that of female, but shorter, 164 × 29 μ, 5.7 times longer than wide.

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 1.0:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 127), so that formula is same as for males of previous four species. Second antenna (Fig. 129) resembling that of female, but small knobs along inner margin of second segment proximal to minute setule.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 130) rather closely resembling that of *L. arcuatipes*. Claw 330 μ along its axis.

Area between maxillipeds and first pair of legs like that of female.

Legs 1–4 resembling those of female, except formula for last segment of endopod of leg 1 (Fig. 131) which is I, I, 4, instead of I, 5 as in female.

Leg 5 (Fig. 132) with elongated straight free segment, 68 × 19 μ (greatest dimensions), with small spinules on outer surface. Two terminal setae 40 μ (outer) and 17 μ (inner), and seta on body near free segment 63 μ. All setae naked.

Leg 6 (Fig. 133) with two small naked setae 18 and 20 μ long.

Spermatophore not seen.

Color in life in transmitted light somewhat more amber than in female, eye red.

Etymology.—The specific name *lobophorus*, from λοβός = a lobe and φορέω = to bear or carry, alludes to the prominent posteroventral lobe on the first postgenital segment in the female (second in male).

Comparison with related species.—The prominent posteroventral lobe on the first postgenital segment of the female (and on the second postgenital segment of the male) distinguishes this species from all other known species of *Lichomolgus*.

By its 3-segmented second antenna (rather than 4-segmented), *L. lobophorus* differs from all species in the genus except *L. compositus* Humes and Frost, 1964, and *L. arcuatipes*. *L. compositus*, though showing a generally similar body form, is unlike the new species in the nature of the setae on the caudal rami, the details of the armature of segment 3 of the second antenna, the form of the mandible (lacking inner digitiform processes), the armature of the second maxilla, and the form of leg 5.

L. lobophorus, being similar to *L. arcuatipes* in many ways (particularly in the form of the mandible), is apparently closely related to it. However, *L. lobophorus* may be distinguished from *L. arcuatipes* by the posteroventral lobe on the postgenital region and by other details such as the number of eggs in the egg sac, the surficial ornamentation of the second segment of the first antenna, the form of the labral lobes, the nature of the outer spines on the exopods of legs 1–4, and the form and ornamentation of leg 5.

Lichomolgus geminus n. sp.

Figs. 134–150

Type material.—141 females and 102 males from *Stylophora pistillata* (Esper) in a depth of 0.5 m, Navetsy, Nosy Bé, Madagascar. Collected September 24, 1964. Holotype female, allotype, and 145 paratypes (90 females and 55 males) deposited in the United States National Museum, 45 paratypes (25 females and 20 males) in the

Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 15 females and 7 males in 0.2 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, June 21, 1963; 9 females and 7 males in 0.5 m, Ambariobe, July 21, 1963; 36 females, 16 males, and 1 copepodid in 0.5 m, Ambariobe, August 4, 1963; 27 females and 21 males in 3 m, Ambariobe, August 13, 1963; 18 females and 8 males in 0.5 m, Ambariobe, October 6, 1963; and 2 females and 1 male in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964. From *Stylophora mordax* (Dana): 21 females, 7 males, and 1 copepodid in 2 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, October 1, 1963. From *Acropora* sp.: 32 females and 6 males in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960.

Female.—Body form (Fig. 134) resembling that of *L. compositus* Humes and Frost, 1964. Length 1.59 mm (1.56–1.61 mm) and greatest width 0.58 mm (0.57–0.59 mm), based on 10 specimens. Ratio of length to width of prosome 1.38:1.

Segment of leg 5 (Fig. 135) 83 × 202 μ. Genital segment 146 × 138 μ, very similar in form to that of *L. compositus*. Areas of attachment of egg sacs dorsolaterally placed, each area (Fig. 136) with two very small setae (4 μ long) and a minute process. Three postgenital segments 125 × 138, 107 × 117, and 88 × 100 μ from anterior to posterior.

Caudal ramus (Fig. 137) greatly elongated, 265 × 29 μ (width taken at middle), tapering slightly distally, 9.1 times longer than wide. Setae short and naked, resembling those of *L. compositus*. Outer lateral seta 50 μ, outermost terminal seta 53 μ, innermost terminal seta 55 μ. Two median terminal setae broadened and hyaline, 68 μ (outer) and 75 μ (inner) in length. Dorsal pedicellate seta 34 μ. Both dorsal and ventral surfaces of ramus with minute hairs. No setule seen on proximal outer margin of ramus.

Egg sac (Fig. 138) small, globular, 244 × 212 μ in dorsal view, containing usually 4 eggs (sometimes 5).

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with a few small hairs. Ratio of length of prosome to that of urosome 1.14:1. (In life the urosome may form a Z-shaped flexure, with the genital segment drawn forward under the metasome and the postgenital segments retained in line with the prosome.)

Rostral area with many long setules as in *L. compositus*.

First antenna segmented and armed as in *L. compositus*, first segment having only a single seta. Lengths of segments: 75 (88 μ along anterior edge), 101, 42, 59, 48, 34, and 25 μ, respectively.

Second antenna, labrum, mandible, paragnath, first maxilla, second maxilla, maxilliped, region between maxillipeds and first leg, leg 1, leg 2, and leg 3 like those of *L. compositus*.

Leg 4 (Fig. 139) segmented and armed as in *L. compositus*, last segment of exopod with the formula II, I, 5. Inner coxal seta naked and 22 μ long. Endopod somewhat longer than in that species; first segment 39 × 32 μ, with its plumose inner seta 65 μ; second segment 99 × 23 μ (length including terminal processes of 5 μ and width taken at widest point), narrowest width 12.5 μ, two terminal fringed spines 40 μ (outer) and 74 μ (inner) in length.

Leg 5 (Fig. 140) with free segment slender and arched, 147 × 14 μ (width taken at narrowest point at junction of first and second thirds), without fine ornamentation. Two terminal setae 26 μ (outer) and 88 μ (inner). Seta on body near insertion of free segment 35 μ. All setae naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 136).

Color in life in transmitted light translucid, eye red, egg sacs light gray.

Male.—Body form (Fig. 141) like that of *L. compositus*. Length 1.49 mm (1.42–

1.55 mm) and greatest width 0.50 mm (0.48–0.51 mm), based on 10 specimens. Ratio of length to width of prosome 1.32:1.

Segment of leg 5 (Fig. 142) 55 × 161 μ. Genital segment 208 × 280 μ, wider than long. Four postgenital segments 57 × 94, 86 × 86, 73 × 82, and 78 × 86 μ from anterior to posterior. Caudal ramus (Fig. 153) similar to that in *L. compositus*, but longer, 229 × 31 μ, 7.4 times longer than wide.

Rostral area, first antenna (with aesthetes arranged as 0, 2, 0, 1, 1, 1, and 1), second antenna, labrum, mandible, paragnath, first maxilla, second maxilla, maxilliped (claw 305 μ along its axis), region between maxillipeds and first leg, and leg 1 (with last segment of endopod having one serrated spine, one setiform spine, and four setae) resembling those of *L. compositus*.

Exopods of legs 2, 3, and 4 as in *L. compositus*. Endopod of leg 2 with outer terminal spine on last segment (Fig. 144) modified as shown in detail in Figure 145. Endopod of leg 3 with outer terminal spine on last segment (Fig. 146) shorter than that in *L. compositus*, but not as greatly modified as in preceding leg. Endopod of leg 4 (Fig. 147) elongated; first segment 39 × 33 μ, with its plumose seta 77 μ; second segment 111 × 27 μ (length including terminal processes of 5 μ and width taken at widest point), narrowest width 12.5 μ, two terminal fringed spines 43 μ (outer) and 79 μ (inner) in length.

Leg 5 (Fig. 148) with elongated rectangular free segment 50 × 12.5 μ, unornamented, its two naked terminal setae 28 μ (outer) and 34 μ (inner) in length.

Leg 6 (Fig. 149) the usual posteroventral flap on genital segment, bearing two small naked setae 23 and 19 μ in length.

Spermatophore (Fig. 150), attached to female, oval, 174 × 107 μ (not including the short neck).

Color in life as in female.

Etymology.—The specific name *geminus*, from Latin = twin-born or similar, refers to the close similarity of this species to *L. compositus*.

Comparison with related species.—*L. geminus* shows three features which in combination serve to distinguish it from all species of *Lichomolgus* except *L. compositus* Humes and Frost, 1964 (associated with the coral *Seriatopora subseriata* Ehrenberg in Madagascar). These are: the presence of only a single seta on segment 1 of the first antenna, a 3-segmented second antenna, and the two short broad hyaline setae on the caudal ramus. *L. lobophorus* and *L. arcuatipes* both have a 3-segmented second antenna, but differ from the new species in having four setae on segment 1 of the first antenna, and in having relatively unmodified setae on the caudal ramus.

L. geminus appears to be very closely related to *L. compositus*, the two species showing striking similarities. There exist, however, several significant differences which are sufficiently important in our opinion to warrant considering these copepods from *Stylophora* as representing a distinct species. In *L. geminus* the endopod of leg 4 is relatively more slender than in *L. compositus*, the free segment of leg 5 in the female is more slender, the caudal ramus is longer and more slender (9.1:1 in the female, 7.4:1 in the male), the egg sac is globular with 4–5 eggs (7 eggs in *L. compositus*), and there is sexual dimorphism in the outer terminal spine on the last segment of the endopods of legs 2 and 3 in the male.

Lichomolgus crassus n. sp.

Figs. 151–182

Type material.—54 females and 27 males from *Stylophora pistillata* (Esper) in a depth of 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected August 4, 1963. Holotype female, allotype, and 61 paratypes (41 females and 20 males) deposited in the United States National Museum, 14 paratypes (10 females and 4 males) in the

Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 1 female and 5 males in 0.2 m, Ambariobe, June 21, 1963; 3 males in 0.5 m, Ambariobe, July 21, 1963; 1 female and 16 males in 0.5 m, Ambariobe, August 13, 1963; 1 female and 10 males in 0.5 m, Ambariobe, October 6, 1963; 3 males in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964; and 1 female and 33 males in 0.5 m, Navetsy, Nosy Bé, September 24, 1964. From *Stylophora mordax* (Dana): 33 males in 2 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, October 1, 1963. From *Acropora* sp.: 15 males in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960.

Female.—Body (Figs. 151 and 152) with broadened and thickened prosome; urosome slender and in life folded under metasome with only postgenital segments visible in dorsal view. Length 1.38 mm (1.32–1.44 mm) and greatest width 0.66 mm (0.60–0.72 mm), based on 10 specimens. Greatest dorsoventral thickness 0.48 mm. Segment of leg 1 clearly set off from head; epimeral areas of metasomal segments as in figures. Ratio of length to width of prosome 1.07:1.

Segment of leg 5 (Fig. 153) 96 × 257 μ. Genital segment (Fig. 153) rather narrow, wider in its anterior third (156 μ) than in its posterior two-thirds (127 μ); its dorsal length (95 μ) much shorter than its ventral length (195 μ). Areas of attachment of egg sacs located dorsolaterally, each area (Fig. 154) with two minute setae about 6 μ in length with a spiniform process between them. First postgenital segment (Fig. 155) shorter dorsally (60 μ) than ventrally (112 μ) and 117 μ wide; second 83 × 96 μ, and third 78 × 98 μ (this last segment apparently without a row of spinules along posteroventral margin).

Caudal ramus (Fig. 156) moderately elongated, 112 × 39 μ, 2.87 times longer than wide. Setae relatively short and naked. Outer lateral seta 41 μ, outermost terminal seta 50 μ, innermost terminal seta 46 μ. Two median terminal setae broadened, 68 μ (outer) and 73 μ (inner) in length. Dorsal pedicellate seta 30 μ. Both dorsal and ventral surfaces of ramus with a few minute hairs and refractile points. No setule seen on proximal outer margin of ramus.

Egg sac unkown.

Dorsal surface of prosome with many refractile points. Dorsal and ventral surfaces of urosome with a few hairs and refractile points. Ratio of length of prosome to that of urosome difficult to establish because of flexure of urosome, but estimated to be about 1.5:1.

Rostral area (Fig. 157) with many hyaline setules. On ventral surface of head a sclerotized ridge extending from insertion of first antenna diagonally toward posterolateral corners of head region.

First antenna (Fig. 158) segmented and armed as in *L. compositus* and *L. geminus*, first segment having only a single seta (in one female first segment of one antenna had an extra seta). Lengths of segments: 66 (84 μ along anterior edge), 70, 40, 35, 42, 21, and 19 μ respectively. All setae short and naked.

Second antenna (Fig. 159) 3-segmented as in *L. compositus*, *L. arcuatipes*, *L. lobophorus*, and *L. geminus*, the dual nature of the slender third segment (formed by fusion of original segments 3 and 4) indicated by three small obtuse hyaline elements (representing the usual three setae on penultimate segment in *Lichomolgus*). Armature: 1, 1, 3 + I + 2 small obtuse elements. Terminal claw short (25 μ along its axis) and reflexed.

Labrum (Fig. 160) with a few hyaline setules, its posteroventral margin bilobed.

Mandible (Fig. 161) resembling that of *L. compositus* and *L. geminus*. Paragnath (Fig. 162) a small somewhat pointed lobe with hairs. First maxilla (Fig. 163), with four elements, second maxilla (Fig. 164), and maxilliped (Fig. 165), resembling those of *L. compositus* and *L. geminus*.

Area between maxillipeds and first pair

of legs (Fig. 166) not protuberant; sclerotized line between bases of maxillipeds not complete.

Legs 1–4 (Figs. 167, 168, 169, and 170) segmented as in previous six species, with same spine and setal formula. Inner coxal seta of leg 4 short, 22 μ in length, and naked; basis of this leg with hairs on inner margin. Spines on exopod of leg 1 lamellate, with short proximal spinules and terminal flagella; these spines on legs 2–4 with smooth lamellae. Endopod of leg 4 moderately elongated. First segment 28×24 μ, with its plumose inner seta 40 μ. Second segment 57×22 μ (greatest dimensions), its terminal spines naked with obtuse tips, outer 33 μ, inner 56 μ in length.

Leg 5 (Fig. 171) with elongated free segment 88×14 μ, only slightly arched and without fine ornamentation. Two terminal setae 24 μ (outer) and 60 μ (inner). Seta on body near insertion of free segment 23 μ. All setae naked.

Leg 6 probably represented by the two small elements near attachment of egg sac (see Figure 154).

Color in life in transmitted light translucid to opaque, reddish amber areas at bases of first antennae and external to insertions of legs, eye red.

Male.—Body (Fig. 172) with prosome less broadened and thickened than in female; urosome not folded under metasome, but extended in a more usual position. Length 1.23 mm (1.20–1.25 mm) and greatest width 0.51 mm (0.50–0.51 mm), based on 10 specimens. Ratio of length to width of prosome 1.2:1.

Segment of leg 5 (Fig. 173) 68×168 μ. Genital segment 177×224 μ, wider than long, with rounded lateral margins. Four postgenital segments 44×91, 64×85, 70×74, and 65×75 μ from anterior to posterior.

Caudal ramus (Fig. 174) similar to that of female, but longer, 149×29 μ, 5.13 times longer than wide.

Rostral area as in female.

First antenna (Fig. 175) segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is same as for males of *L. compositus* and *L. geminus*.

Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla resembling those of female. Maxilliped (Fig. 176) segmented and armed as in previous species. Claw 145 μ along its axis (including lamella), showing a distinct line of division about midway, and having hyaline serrations along concave margin.

Area between maxillipeds and first pair of legs like that of female.

Legs 1–4 with same spine and setal formula as in female. Leg 1 (Fig. 177) with spines on exopod and single spine on endopod much more strongly barbed than in female. Legs 2 and 3 with spines on exopods moderately barbed, those on endopod of leg 2 as in Figure 178, and on endopod of leg 3 as in Figure 179. Leg 4 with spines on exopod slightly barbed. Endopod (Fig. 180) longer than in female; first segment 30×31 μ, with its plumose inner seta 58 μ; second segment 75×25 μ, more attenuated than in female, with its two terminal spines 37 μ (outer) and 66 μ (inner) in length.

Leg 5 (Fig. 181) with straight and moderately short free segment, 35×10 μ, without fine ornamentation. Two terminal naked setae 23 and 37 μ long.

Leg 6 (Fig. 182) a posteroventral flap on genital segment, bearing two small naked setae 20 and 17 μ in length.

Spermatophore seen only partly developed inside body of male (Fig. 182).

Color in life resembling that of female.

Etymology.—The specific name *crassus*, from Latin = thick or solid, alludes to the broadened and thickened prosome.

Comparison with related species.—*L. crassus* may be distinguished from all but four species of *Lichomolgus* by its 3-segmented second antenna (resulting from a fusion of segments 3 and 4). These four species are: *L. compositus* Humes and Frost, 1964, *L. arcuatipes*, *L. lobophorus*, and *L. geminus*. Two of these, *L. arcuatipes* and *L. lobophorus*, differ from the

new species in having four setae (instead of one) on the first segment of the first antenna and in having four small fingerlike processes on the basal part of the mandible. The other two, *L. compositus* and *L. geminus*, differ in showing sexual dimorphism in the formula for leg 1 (last segment of endopod I, 5 in the female, I, I, 4 in the male) and in having a less broadened prosome (ratio of length to width in female of *L. compositus* 1.27:1, in *L. geminus* 1.38:1).

On the basis of several points of similarity in *L. crassus*, *L. compositus*, and *L. geminus*, such as the setulose rostral area, the single seta on the first segment of the first antenna, the structure of the mandible, and the two broadened and relatively short terminal setae on the caudal ramus, these three species appear to be closely related.

Lichomolgus actinophorus Humes and Frost, 1964

This species has been previously reported (Humes and Frost, 1964) from *Pavona angulata* Klunzinger and *Pavona cactus* (Forskål) in Madagascar. New host records are:

1) From *Pavona danai* (Milne Edwards and Haime): 31 females and 29 males in 10 cm, Ambariobe, near Nosy Bé, October 6, 1963; 189 females and 193 males in 10 cm, Boloboxo, Nosy Faly, east of Nosy Bé, August 10, 1964.

2) From *Pavona danai* or *Pavona angularis* (Klunzinger): 111 females and 87 males in 1 m, Ambariobe, September 6, 1963. Identification of host uncertain.

3) From *Pavona*? *venusta* (Dana): 28 females and 22 males in 1 m, Ambariobe, September 17, 1963.

Lichomolgus compositus Humes and Frost, 1964

This species has been known only from *Seriatopora subseriata* Ehrenberg in Madagascar (Humes and Frost, 1964). It is now reported as follows:

1) From *Seriatopora octoptera* Ehrenberg: 14 females and 2 males in 2 m, Pte. Ambarionaomby, Nosy Komba, August 18, 1960.

2) From *Seriatopora* sp.: 8 females and 2 males in 1 m, Pte. Ambarionaomby, January 12, 1964.

Monomolgus unihastatus Humes and Frost, 1964

This lichomolgid has been reported only from *Porites* sp. cf. *P. andrewsi* Vaughan in Madagascar (Humes and Frost, 1964). It is now recorded from *Porites* sp. cf. *P. nigrescens* Dana (111 females and 93 males in 1 m, Pte. de Tafondro, Nosy Bé, September 19, 1963).

Kombia angulata Humes, 1962

This copepod has been previously known only from *Psammocora* sp. in Madagascar (Humes, 1962). New host records are:

1) From *Porites* (s. g. *Synaraea*) sp.: 19 females and 43 males in 1 m, Pte. Ambarionaomby, Nosy Komba, November 28, 1963; 28 females and 28 males in 1 m, Pte. Lokobe, Nosy Bé, November 29, 1963; 6 females and 32 males in 2 m, northern end of Nosy Sakatia, an island close to the western shore of Nosy Bé, August 19, 1963; 4 females in 1 m, Ambariobe, near Nosy Bé, September 17, 1963; 10 females and 14 males in 2 m, northern end of Nosy Sakatia, September 18, 1963; 8 females and 10 males in 1 m, Pte. de Tafondro, Nosy Bé, October 2, 1963; 102 females and 153 males in 1 m, Pte. Lokobe, November 30, 1963; and 7 females and 8 males in 1–2 m, Ankify, on the mainland of Madagascar, near Nosy Komba, December 30, 1963.

2) From *Porites* sp. cf. *P. nigrescens* Dana: 1 female and 1 male in 1 m, Pte. de Tafondro, September 19, 1963.

3) From *Porites*, young colony: 3 females and 5 males in 1 m, Pte. de Tafondro, September 19, 1963.

Although Humes (1962) indicated that the genus *Kombia* should probably be placed in the Xarifiidae, it would now seem

that *Kombia* belongs instead to the Lichomolgidae. The discovery of certain new genera of the Lichomolgidae since 1962 has widened our concept of the family. The mouthparts of *Kombia* are essentially lichomolgid in form, though the flagellum of the mandible is relatively short compared to most other genera. A somewhat similar short flagellum is present in other lichomolgids, for example, *Monomolgus unihastatus* Humes and Frost, 1964, and *Rhynchomolgus corallophilus* Humes and Ho, 1967a. The tendency in *Kombia* toward reduction of legs 1–5, beginning at the posterior end of the series, is seen also in *Rhynchomolgus* (where it is even more strongly expressed). Since the limits of the Lichomolgidae, as we see them, now include such transformed genera as *Rhynchomolgus*, it does not seem inconsistent to include *Kombia* in this family.

PRIONOMOLGUS n. gen.

Type and only known species: *Prionomolgus lanceolatus* n. sp.

Body cyclopoid. Segment of leg 1 in female separated from head by a dorsal and lateral furrow, in male lacking this separation. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with six setae. First antenna 7-segmented, with lichomolgid setation. Second antenna 3-segmented. Mouthparts lichomolgid. Mandible with proximal region having two strongly serrated lobes on concave edge; flagellum relatively short. Paragnath a small nearly naked lobe. First maxilla with three setae. Second maxilla 2-segmented. Maxilliped in female 3-segmented, in male 4-segmented (fourth segment probably forming part of terminal claw).

Legs 1–4 with 3-segmented rami, except for endopod of leg 4 which is 2-segmented. Leg 1 in male showing sexual dimorphism, formula for last segment of endopod being I, I, 4, instead of I, 5 as in female. Endopod of leg 4 with formula 0–1; I. Leg 5 with free segment bearing two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Gender masculine.

Etymology.—The generic name is a combination of πρίων = a saw (alluding to the serrated lobes on the mandible) and μολγός = a sack made of leather.

Prionomolgus lanceolatus n. gen., n. sp.

Figs. 183–210

Type material.—31 females, 67 males, and 23 copepodids from *Pachyseris speciosa* (Dana) in a depth of 3 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected September 3, 1963. Holotype female, allotype, and 79 paratypes (25 females and 54 males) deposited in the United States National Museum, 13 paratypes (3 females and 10 males) in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Pachyseris speciosa* in 2 m, Ambariotsimaramara, an islet on the southern shore of Nosy Bé, between Pte. Mahatsinjo and Ampombilava).—6 females, 9 males, and 4 copepodids, October 18, 1963; 2 females and 1 male, June 12, 1964.

Female.—Body (Fig. 183) with flattened and broadened prosome. Length 1.36 mm (1.26–1.42 mm) and greatest width 0.85 mm (0.77–0.91 mm), based on 10 specimens. Ratio of length to width of prosome about 1:1. Segment of leg 1 separated from head dorsally and laterally by a furrow. Epimeral areas of segments of legs 1–3 expanded, those of segment of leg 4 short and pointed.

Segment of leg 5 (Fig. 184) 55 × 263 μ. Between this segment and genital segment no ventral intersegmental sclerite discernible. Genital segment broadened in its anterior fourth and tapered posteriorly, its greatest dimensions being 166 × 245 μ, wider than long. Areas of attachment of egg sacs situated dorsolaterally, each area (Fig. 185) with two minute setae 5 μ in

length. Three postgenital segments 83 × 92, 68 × 88, and 78 × 90 μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side and two short rows of similar spinules posterodorsally near insertion of ramus (see Figure 186).

Caudal ramus (Fig. 186) moderately elongated, 100 × 39 μ, 2.56 times longer than wide. Outer lateral seta 100 μ and naked, outermost terminal seta 105 μ with a few proximal hairs, innermost terminal seta 113 μ with proximal hairs. Two long median terminal setae 340 μ (inner) and 230 μ (outer), both with very short barbules along their midregions. Dorsal pedicellate seta short, 40 μ, and haired. Dorsal and ventral surfaces of ramus with short hairs and refractile points.

Dorsal surface of prosome with many refractile points and a few hairs; dorsal and ventral surfaces of urosome with a few refractile points. Ratio of length of prosome to that of urosome 1.84:1.

Egg sac (Fig. 187) oval, 363 × 242 μ, containing about 15 eggs, each 94–104 μ in diameter.

Rostral area (Fig. 188) weakly developed, without a definite posteroventral margin.

First antenna (Fig. 189) slender, 376 μ long, and 7-segmented, with a sclerite on third segment suggesting an intercalary segment. Lengths of segments: 42 (86 μ along anterior margin), 141, 26, 42, 39, 27, and 15 μ respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many species of *Lichomolgus*. Several setae on last three segments distally haired as in figure.

Second antenna (Fig. 190) slender and 3-segmented, the last segment representing the fusion of two original segments (dual nature of this segment indicated by presence of three small setae corresponding to those usually found on segment 3 in other lichomolgids). Armature: 1, 1, 3 + I + 1 small hyaline element. Terminal claw short, about 24 μ along its axis.

Labrum (Fig. 191) with two posteroventral lobes having broad medial hyaline margins.

Mandible (Fig. 192) with proximal region separated into two parts by a constriction. Distal area beyond constriction having on its convex side a short row of spinules followed by a triangular process and then by a row of small spinules; on its concave side two lobes with strongly serrated margins. Flagellum relatively short with lateral serrations. Paragnath (Fig. 193) a small lobe, naked except for a single small setule. First maxilla (Fig. 194) having three elements with serrated flanges. Second maxilla (Fig. 195) 2-segmented. First segment unarmed. Second segment with its outer (ventral) margin bearing a minute proximal spinule and a distal spinulose seta, with its inner (dorsal) margin carrying a blunt seta with hyaline lamellae; terminal lash with long proximal spinules and distal serrations. Maxilliped (Fig. 196) 3-segmented; first segment unarmed, second with two sparsely barbed inner setae, and third with two setae (one small and naked, the other larger and barbed) and terminating in a slender barbed spiniform process.

Area between maxillipeds and first pair of legs (Fig. 188) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 197, 198, 199, and 200) with trimerous rami, except for endopod of leg 4 which is 2-segmented. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, 1, 5 end 0–1; I

Inner coxal seta long and haired in legs 1–3, but in leg 4 only 6 μ long and naked. Hairs on inner margin of basis in all four legs. Outer spines on exopod of leg 1 with

coarsely spinulose lamellae and having flagella; those of legs 2–4 with finely spinulose lamellae and without flagella. Endopod of leg 4 (Fig. 201) with hairs along outer margins of both segments. First segment 22 × 14 μ (greatest dimensions), its plumose inner seta 56 μ long. Second segment 26 × 9 μ (greatest dimensions), somewhat narrowed distally, its single terminal spine 33 μ long with narrow hyaline lamellae.

Leg 5 (Fig. 202) having a moderately elongated free segment 84 μ long, 25 μ wide at the level of proximal inner expansion and 17 μ wide halfway from the outer marginal notch to the end. Two terminal naked setae 60 and 77 μ in length. Outer surface of segment with small spinules. Seta on body near free segment 77 μ long and naked; a row of spinules near this seta.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 185).

Color in life in transmitted light translucid, eye dark red, egg sacs gray.

Male.—Body (Fig. 203) with broad flattened prosome nearly as in female. Length 1.04 mm (0.99–1.08 mm) and greatest width 0.53 mm (0.49–0.55 mm), based on 10 specimens. Ratio of length to width of prosome 1.12:1. Segment of leg 1 not separated from head by a furrow. Epimeral areas of metasomal segments as in female.

Segment of leg 5 (Fig. 204) 26 × 172 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment broader than long, 208 × 270 μ, its lateral borders sclerotized and rounded anteriorly but hyaline and crenated posteriorly. Four postgenital segments 36 × 70, 42 × 67, 40 × 63, and 61 × 67 μ from anterior to posterior.

Caudal ramus resembling that of female, but smaller, 88 × 31 μ, with hairs on setae fewer than in female (see Figure 204).

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 1.33:1.

Rostral area like that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 205) slender and 4-segmented, assuming that the proximal part of claw represents a fourth segment. First segment unarmed, second with two naked setae and two rows of spinules on its inner surface, third small and unarmed. Claw elongated, slender, and recurved, 196 μ along its axis (including terminal lamella), with weak indication of division about midway; proximally with two unequal setae, the smaller seta naked, the larger with distal spinules.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented and armed as in female, except for last segment of endopod of leg 1 where formula is I, I, 4 (Fig. 206), instead of I, 5 as in female. Endopod of leg 4 (Fig. 207) with second segment relatively shorter than in female; first segment 15 × 11 μ, with its plumose inner seta 41 μ, and second segment 17.5 × 8 μ, with its terminal spine 28 μ.

Leg 5 (Fig. 208) with free segment 42 × 9 μ, lacking an inner proximal expansion, with outer marginal notch less evident than in female, and with fewer outer spinules than in opposite sex. Two terminal setae 28 and 48 μ; seta on body near insertion of free segment 56 μ.

Leg 6 (Fig. 209) consisting of a posteroventral flap on genital segment, bearing two slender naked setae 33 and 38 μ long.

Spermatophore (Fig. 210), attached to female in a pair, about 200 × 95 μ (not including the neck).

Color in life similar to that of female.

Etymology.—The specific name *lanceolatus*, from the Latin word *lanceola* = a small lance, refers to the single terminal spine on the endopod of leg 4.

Comparison with other lichomolgids.—In the Lichomolgidae eight genera have a 2-segmented endopod in leg 4. These are: *Lichomolgus* Thorell, 1860, *Epimolgus* Bocquet and Stock, 1956, *Gelastomolgus* Humes, in press, *Indomolgus* Humes and Ho, 1967c, *Lichomolgides* Gotto, 1954, *Monomolgus* Humes and Frost, 1964, *Nasomolgus* Sewell, 1949, and *Stellicola* Kossmann, 1877. (*Macrochiron* Brady, 1872, has a 1-segmented endopod which may be partially divided.) Of these only *Gelastomolgus* has the formula for the endopod of leg 4 as 0–1; 1, thus resembling *P. lanceolatus*.

The new genus and species differs, however, from *Gelastomolgus spondyli* Humes, in press, in several important respects. In *G. spondyli* the body form is rather modified from the usual cyclopoid type, the second antenna is 4-segmented, the mandible has a broad elongated blade and lacks serrated lobes, the maxilliped of the female is apparently 2-segmented and much modified, and leg 1 has the same formula in both sexes.

The mandible of *P. lanceolatus*, although basically lichomolgid in form, differs from that in all other genera in the family. In no other genus do the two lobes on the concave side of the basal part of the mandible possess strongly serrated margins; in those genera where such lobes occur they are ornamented with spinules or hairs.

Since there seems to be no known genus in the Lichomolgidae which could receive the new species from *Pachyseris* without radically broadening the generic concept, we have concluded that the species represents a new genus, basing our judgment primarily on the nature of the mandible and the form and armature of the endopod of leg 4.

HAPLOMOLGUS n. gen.

Type and only known species: *Haplomolgus montiporae* n. sp.

Body cyclopoid. Segment of leg 1 fused with head. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with six setae. First antenna 7-segmented, with lichomolgid setation. Second antenna 4-segmented. Mouthparts lichomolgid.

Legs 1–4 with 3-segmented rami, except for endopod of leg 4 which is composed of a single unarmed segment, often bearing a small rounded terminal lobe. Leg 5 with a large free segment armed with two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Etymology.—The generic name is a combination of ἁπλόος = single (alluding to the 1-segmented unarmed endopod of leg 4) and μολγός = a sack made of leather. Gender masculine.

Haplomolgus montiporae n. gen., n. sp.

Figs. 211–240

Type material.—147 females and 81 males from *Montipora sinensis* Bernard in a depth of 1 m, Nosy Taolankena, a small island on the northwestern side of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 140 paratypes (90 females and 50 males) deposited in the United States National Museum, 45 paratypes (30 females and 15 males) in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Montipora* sp.: 58 females and 19 males in 1 m, west of Pte. de Tafondro, Nosy Bé, December 3, 1963; 165 females and 66 males in 3 m, western side of Nosy Komba, near Nosy Bé, October 19, 1964. From *Montipora* sp. cf. *M. stellata* Bernard: 27 females and 12 males in 2 m, Ampombilava, Nosy Bé, September 26, 1964.

Female.—Body (Fig. 211) rather slender, with prosome moderately thickened dorsoventrally. Length 0.86 mm (0.83–0.89 mm) and greatest width 0.27 mm (0.26–0.29 mm), based on 10 specimens. Ratio of length to width of prosome 1.5:1. Segment of leg 1 not separated from head. Epimeral areas

of metasomal segments only moderately expanded.

Segment of leg 5 (Fig. 212) 101 × 146 μ. Genital segment 112 × 96 μ, only a little longer than wide and slightly wider in its anterior half than posteriorly. Areas of attachment of egg sacs located dorsally, each area (Fig. 213) with two small setae 4 μ long. Three postgenital segments (Fig. 214) 65 × 65, 78 × 55, and 37 × 55 μ from anterior to posterior, the middle segment being the longest. Edge of anal operculum with a row of minute spinules.

Caudal ramus (Fig. 215) moderately elongated, 48 × 21 μ, about 2.3 times longer than wide. Outer lateral seta 54 μ, outermost terminal seta 58 μ, innermost terminal seta 77 μ. Two long median terminal setae 218 μ (inner) and 156 μ (outer). Dorsal pedicellate seta 73 μ. All setae naked. A few hairs on dorsal surface of ramus.

Dorsal surface of prosome and urosome with a few hairs. Ratio of length of prosome to that of urosome 1.21:1.

Egg sac (Fig. 211) approximately 215 × 133 μ, containing two large eggs 107–133 μ in diameter.

Rostrum (Fig. 216) well formed, extending as a tongue-shaped raised area between bases of antennae. Between rostrum and labrum a small raised keel-like area.

First antenna (Fig. 217) slender, 203 μ long, and 7-segmented. Lengths of segments: 17 (35 μ along anterior margin), 64, 18, 19, 30, 22, and 15 μ respectively. Formula for armature: 4, 13 (5 + 2 +6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many lichomolgids. All setae naked.

Second antenna (Fig. 218) 4-segmented. Armature: 1, 1, 3, I. Last segment 28 μ along outer side, 15 μ along inner side. Terminal claw 23 μ along its axis.

Labrum (Figs. 216 and 219) with its free edge having two widely divergent narrow lobes. Immediately dorsal to posteromedian area of labrum two pairs of small spiniform processes.

Mandible (Fig. 220) with an unusually slender proximal part and broadened distal part, the two areas separated by a constricted neck. Distal part bearing on its convex side a large pointed posteriorly directed process (partly hyaline) followed by a row of small serrations, and on its concave side two lobes, each with a row of slender and slightly obtuse spinules. Flagellum moderately long, with lateral spinules distally. Paragnath (Fig. 221) a small lobe with a few hairs. First maxilla (Fig. 222) a single segment with four elements, three finely spinulose setae and a smaller naked seta. Second maxilla (Fig. 223) 2-segmented. First segment with a minute spinule. Second segment bearing on its outer (ventral) margin a minute proximal spinule and a distal lamellate seta and on its inner (dorsal) margin a seta with a row of minute spinules; terminal lash with a row of dentiform spinules becoming more slender distally. Maxilliped (Fig. 224) 3-segmented; first segment unarmed, second with two very unequal setae, and third with two setae (one large and barbed, the other small and naked) and terminating in a barbed spiniform process.

Area between maxillipeds and first pair of legs not protuberant and formed as in Figure 216. Immediately anterior to this area and between second maxillae a median minutely setose lobe.

Legs 1–4 (Figs. 225, 226, 227, and 228) with trimerous rami, except for endopod of leg 4 which has only a single segment. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0–1; 0–2; II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0

Inner coxal seta long and haired in legs 1–3, but in leg 4 only 7 μ long and naked. Hairs on inner margin of basis in all four legs. Endopod of leg 3 (Fig. 227) with last segment having formula of II, 2, in-

stead of I, II, 2 as often seen in other lichomolgid genera. Endopod of leg 4 (Fig. 229) a single small unarmed segment 17 × 9 μ, bearing a few outer hairs. Often on this endopod a small distal hyaline lobe is present (Figs. 230 and 231), probably not representing a segment.

Leg 5 (Fig. 232) with a broad free segment 85 × 40 μ, its inner surface slightly concave, and armed with two terminal naked setae 39 and 44 μ long. Between these two setae a patch of minute spinules. Seta on body near free segment 46 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 213).

Color in life in transmitted light slightly amber, eye red, egg sacs grayish black.

Male.—Body (Fig. 233) resembling in general form that of female. Length 0.87 mm (0.81–0.90 mm) and greatest width 0.28 mm (0.27–0.29 mm), based on 10 specimens. Ratio of length to width of prosome 1.43:1. Segment of leg 1 fused with head. Epimeral areas of metasomal segments as in female.

Segment of leg 5 (Fig. 234) 49 × 112 μ. Genital segment 169 × 156 μ, only slightly longer than wide, its lateral borders gently rounded in dorsal view. Four postgenital segments 44 × 56, 53 × 51, 63 × 48, and 34 × 51 μ from anterior to posterior, the next to the last segment being the longest, as in the female.

Caudal ramus resembling that of female, 43 × 22 μ.

Dorsal surface of body ornamented much like that of female. Ratio of length of prosome to that of urosome 1:1.

Rostrum similar to that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4 (their positions indicated by arrows in Figure 217), so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 235) slender and 4-segmented, assuming that the proximal part of claw represents a fourth segment. First segment unarmed, second with two naked setae and two rows of spinules on its inner surface, third small and unarmed. Claw long, slender, and recurved, 156 μ along its axis, with weak indication of division about midway. Proximal part of claw with two unequal setae, the smaller seta naked, the larger with distal spinules; terminal lamella long and narrow.

Area between maxillipeds and first pair of legs as in female. Small median lobe between second maxillae as in that sex.

Legs 1–4 segmented and armed as in female, but slight sexual dimorphism in endopods of legs 1–3. Endopod of leg 1 (Fig. 236) with third segment relatively longer than in female and with outermost seta short (less than length of segment). Endopod of leg 2 (Fig. 237) with third segment broader, two terminal spiniform processes longer, and inner terminal spine relatively shorter than in female. Endopod of leg 3 (Fig. 238) with third segment relatively shorter and broader than in female. Endopod of leg 4 as in female. Outer seta on basis of leg 1 with proximal lateral hairs.

Leg 5 (Fig. 239) with free segment smaller and narrower than in female, 24 × 11 μ, its two terminal setae 11 and 28 μ long. Three small patches of minute spinules as indicated in figure. Seta on body near base of free segment 60 μ long. All setae naked.

Leg 6 (Fig. 240) a posteroventral flap on genital segment, bearing two naked setae 31 and 38 μ long.

Spermatophore not observed.

Color in life as in female.

Etymology.—The specific name *montiporae* is based on the generic name of the host.

Comparison with other lichomolgids.—We interpret the endopod of leg 4 of *Haplomolgus* as being 1-segmented, though the presence in some specimens of a small hya-

line terminal lobe might suggest a reduced second segment. This lobe is not always present, however. In three females and one male it was seen on both endopods, in five females and five males on only one endopod, and in two females and one male it was absent.

There are five lichomolgid genera in which the endopod of leg 4 is 1-segmented, namely, *Kelleria* Gurney, 1927, *Lichomolgella* Sars, 1918, *Octopicola* Humes, 1957, *Paramacrochiron* Sewell, 1949, and *Pseudanthessius* Claus, 1889. In these, however, the endopod is elongated and always provided with setae or spines, while in *Haplomolgus* the endopod is rather oval and unarmed (the few minute hairs along the outer margin being regarded as ornamentation rather than as armature). The mandible in these five genera does not have the large pointed posteriorly directed process seen in *Haplomolgus*.

In *Heteranthessius* T. Scott, 1903, the endopod of leg 4 is reduced to a minute knob, leg 5 is rudimentary with only two setae, and the mandible lacks the large process characteristic of *Haplomolgus*.

On the basis of the nature of the endopod of leg 4 the new genus appears to occupy a position between the group of five genera mentioned above and *Heteranthessius*. The unarmed 1-segmented endopod of leg 4 serves to distinguish *Haplomolgus* from all other lichomolgid genera known to us.

RAVAHINA n. gen.

Type and only known species: *Ravahina tumida* n. sp.

Female.—Body transformed, with swollen prosome. Segment of leg 1 weakly delimited from head. Urosome 5-segmented. Caudal ramus with six elements. First antenna 7-segmented. Second antenna 4-segmented. Mouthparts lichomolgid. Mandible with a small terminal spiniform process apparently representing a much reduced flagellum. First maxilla with three elements. Second maxilla 2-segmented. Maxilliped 3-segmented.

Legs 1 and 2 with 3-segmented rami; legs 3 and 4 with 3-segmented exopods but endopods represented only by a small unsegmented knoblike process. Leg 5 with free segment bearing two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Male.—Unknown.

Etymology.—The generic name is formed from Ravahiny, the name of a queen of the Sakalava, who reigned at Majunga in Madagascar about 1800. Gender feminine.

Ravahina tumida n. gen., n. sp.
Figs. 241–259

Type material.—2 females from *Porites* sp. cf. *P. andrewsi* Vaughan in a depth of 2 m, Pte. Lokobe, Nosy Bé, Madagascar. Collected September 2, 1960. One of these females is the holotype, the other (dissected) a paratype. Also one paratypic female and one immature specimen from *Porites* sp. cf. *P. andrewsi* in 3 m, Pte. de Tafondro, Nosy Bé (about five kilometers east of Pte. Lokobe). Collected September 28, 1960. Holotype and one paratype deposited in the United States National Museum, dissected paratype and immature specimen in the collection of A. G. Humes.

Other specimen.—1 female from *Porites* sp. cf. *P. andrewsi* in 2 m, Pte. de Tafondro, August 29, 1960.

Female.—Body (Figs. 241 and 242) with expanded and swollen prosome. Urosome relatively slender and sometimes contracted. Dimensions of two uncontracted specimens 1.97 × 1.15 mm and 1.67 × 1.10 mm. Ratio of length to width of prosome about 1.1:1. Segment of leg 1 weakly delimited from head.

Segment of leg 5 (Fig. 243) 91 × 363 μ. Genital segment broad, 173 × 363 μ, with rounded lateral borders in dorsal view. Areas of attachment of egg sacs located dorsally, each area (Fig. 244) with two minute setae 3 μ long. Three postgenital

segments 70 × 213, 73 × 180, and 104 × 208 μ from anterior to posterior, the last segment expanded in its posterior two-thirds.

Caudal ramus (Fig. 245) moderately elongated, 159 × 65 μ in greatest dimensions, about 2.45 times longer than wide. All setae naked and all spiniform except dorsal pedicellate seta which is slender and 34 μ long. Outer lateral seta 32 μ, outermost terminal seta 28 μ, innermost terminal seta 18 μ, and two median terminal setae 47 μ (inner) and 33 μ (outer). A few small hyaline setules on dorsal surface of ramus.

Dorsal surface of prosome with minute refractile irregularities (Fig. 246) in the cuticula. Dorsal and ventral surfaces of urosome almost entirely lacking ornamentation. Ratio of length of prosome to that of urosome 1.85:1.

Egg sac unknown.

Rostral area (Fig. 247) weakly developed.

First antenna (Fig. 248) slender, 393 μ long, and 7-segmented. Lengths of segments: 24 (64 μ along anterior edge), 106, 38, 44, 65, 40, and 36 μ respectively. Formula for armature: 3, 14 (6 + 8), 5, 4, 5, 2 + 1 aesthete, and 7 + 1 aesthete. All setae naked.

Second antenna (Fig. 249) 4-segmented. Last segment 77 μ along outer edge, 44 μ along inner edge. Armature: 1, 1, 3, 6 + I. Terminal claw 46 μ along its axis; adjacent long seta (jointed and somewhat spiniform) 56 μ.

Labrum (Fig. 250) with two slightly truncated posteroventral lobes.

Mandible (Fig. 251) with distal part (beyond slight constriction) bladelike, its convex side with two small surficial lobes and a distal marginal serrated fringe, its concave edge with a row of prominent spines. Tip of mandible forming a small spiniform process, perhaps representing the flagellum usually present in lichomolgids. Paragnath not observed. First maxilla (Fig. 252) a small lobe with three terminal elements. Second maxilla (Fig. 253) 2-segmented. First segment unarmed. Second segment with a minute proximal setule on its outer (ventral) margin, a naked seta on its distal anterior surface, and a strongly spinulose distal area on its inner (dorsal) margin, the segment terminating in a lash (apparently only partially articulated with the segment) bearing a row of strong spines. Maxilliped (Fig. 254) 3-segmented; first segment unarmed, second with two very unequal naked setae, and third with two barbed spines (the distal one possibly lacking an articulation and thus being a process rather than a spine) and two small naked setae.

Area between maxillipeds and first pair of legs not protuberant. Without sclerotization between bases of maxillipeds.

Leg 1 (Fig. 255) and leg 2 (Fig. 256) with 3-segmented rami, leg 3 (Fig. 257) and leg 4 (Fig. 258) with 3-segmented exopods but endopods reduced to a small process. Armature as follows:

P_1	protopod 0–0; 1–0	exp I–(1); I–1; II, II, 2 end 0–0; 0–0; I, 2
P_2	protopod 0–0; 1–0	exp I–(2); I–1; II, II, 1 end 0–0; 0–1; II
P_3	protopod 0–0; 1–0	exp I–0; I–1; II, II, 1 end –
P_4	protopod 0–0; 1–0	exp I–0; I–1; II, II end –

All four legs without inner coxal seta and without inner marginal hairs on basis. First segment of exopod of leg 1 with an inner setule (probably to be considered as ornamentation rather than as a part of the armature); two such setules in leg 2, but these setules absent in legs 3 and 4. Both first and second segments of endopod of leg 1 and first segment of endopod of leg 2 lacking the inner seta usually seen in lichomolgids. Endopod of legs 3 and 4 consisting of a small knoblike unornamented and unsegmented process lacking a definite articulation with the basis. Intercoxal plates in all four legs wide and short as in leg 1.

Leg 5 (Fig. 259) with a moderately elongated free segment, 73 × 30 μ, of somewhat irregular outline. Two terminal naked

setae 36 and 19 μ in length. Seta on body near free segment 34 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 244).

Color in life in transmitted light somewhat opaque, eye red.

Male.—Unknown.

Etymology.—The specific name *tumida*, from Latin = swollen, refers to the tumid prosome.

Comparison with other lichomolgids.—*Ravahina tumida* apparently belongs to the family Lichomolgidae. Its mandible lacks the long flagellum characteristic of many lichomolgid genera, but shows a small terminal spiniform process which may represent a very reduced flagellum. (Reduction of the flagellum to a lesser extent is seen in lichomolgids such as *Monomolgus unihastatus* Humes and Frost, 1964, *Kombia angulata* Humes, 1962, and *Rhynchomolgus corallophilus* Humes and Ho, 1967a.) The other mouthparts are essentially lichomolgid in their form.

The first antenna and legs 1–4 have an armature somewhat different from that in many lichomolgid genera. However, in certain transformed lichomolgid genera such as *Kombia* Humes, 1962, *Heteranthessius* T. Scott, 1903, *Rhynchomolgus* Humes and Ho, 1967a, and *Temnomolgus* Humes and Ho, 1967c, the armature of these appendages may not conform to the more "typical" arrangement seen in untransformed lichomolgids (for example, *Lichomolgus* Thorell, 1860).

Evidence for placing *Ravahina* in the Lichomolgidae would be more conclusive if the structure of the male were known. On the basis of our knowledge of the female, however, we think that the new genus should be provisionally considered as belonging to the Lichomolgidae.

Key to the Seventeen Genera of Lichomolgidae Known from the Vicinity of Nosy Bé, Madagascar

1. Legs 1 and 2 with both rami 3-segmented 2
   Legs 1 and 2 with one or both rami reduced to two segments 13
2. Leg 3 with both rami 3-segmented 3
   Leg 3 with one or both rami reduced 15
3. Leg 4 with endopod 3-segmented 4
   Leg 4 with endopod of one or two segments 5
4. Second antenna with claw on third segment; on holothurians ..... *Scambicornus* Heegaard, 1944
   Second antenna with terminal claws on fourth segment; in mantle cavity of pelecypods ..... *Modiolicola* Aurivillius, 1882
5. Leg 4 with endopod 2-segmented, with a distinct line of segmentation between the segments 6
   Leg 4 with endopod 1-segmented 16
6. Second antenna 3-segmented 7
   Second antenna 4-segmented 9
7. Second segment of endopod of leg 4 with two elements; third and fourth segments of second antenna fused to form an apparent single segment; on corals ..... *Lichomolgus* Thorell, 1860 (in part)
   Second segment of endopod of leg 4 with one or three elements 8
8. Mandible with proximal region having two outer serrated lobes; second antenna with a single terminal claw; second segment of endopod of leg 4 with a single spine; on corals ..... *Prionomolgus* n. gen.
   Mandible with proximal region having a row of setae or spines; second antenna with 1, 2, or 3 terminal claws; second segment of endopod of leg 4 with three elements; on asteroids ..... *Stellicola* Kossmann, 1877
9. Endopod of leg 4 with a single element on second segment 10
   Endopod of leg 4 with more than one element on second segment 11
10. First segment of endopod of leg 4 with an inner seta; body rather transformed; in mantle cavity of pelecypods ..... *Gelastomolgus* Humes (in press)
    First segment of endopod of leg 4 unarmed; body typically cyclopoid; on corals ..... *Monomolgus* Humes and Frost, 1964
11. Endopod of leg 4 with two elements on second segment 12
    Endopod of leg 4 with four or five elements (spines or setae) on last segment, formula variable; in zoanthids ..... *Indomolgus* Humes and Ho, 1967c
12. With a pair of setae on anterior part of labrum; maxilliped in female with a long slender last segment; on polychaetes ..... *Nasomolgus* Sewell, 1949
    Without a pair of setae on labrum; maxilliped in female with short last segment; in mantle cavity of pelecypods, on sea anemones, corals, alcyonarians, zoan-

thids, nudibranchs ..... *Lichomolgus* Thorell, 1860 (in part)

13. Both rami of legs 1 and 2 two-segmented; in corals ..... *Rhynchomolgus* Humes and Ho, 1967a
    In legs 1 and 2 exopods 3-segmented, endopods 2-segmented 14
14. Endopod of leg 3 and entire leg 4 absent; in corals ..... *Kombia* Humes, 1962
    Endopod of leg 3 present; leg 4 with 3-segmented rami; on holothurians ..... males of *Scambicornus* Heegaard, 1944
15. Leg 3 with 3-segmented exopod, endopod a small process; in corals ..... females of *Ravahina* n. gen.
    Leg 3 represented only by two setae; in zoanthids ..... *Temnomolgus* Humes and Ho, 1967c
16. Leg 5 with a distinct segment 17
    Leg 5 without a distinct segment; on echinoids, polychaetes ..... *Pseudanthessius* Claus, 1889
17. Second antenna 3-segmented, with large terminal denticulated claw and sometimes an unguiform seta; on hydroids ..... *Macrochiron* Brady, 1872
    Second antenna 4-segmented 18
18. Last segment of second antenna with four claws; endopod of leg 4 with three elements; on cephalopods ..... *Octopicola* Humes, 1957
    Last segment of second antenna with one claw; endopod of leg 4 unarmed; on corals ..... *Haplomolgus* n. gen.

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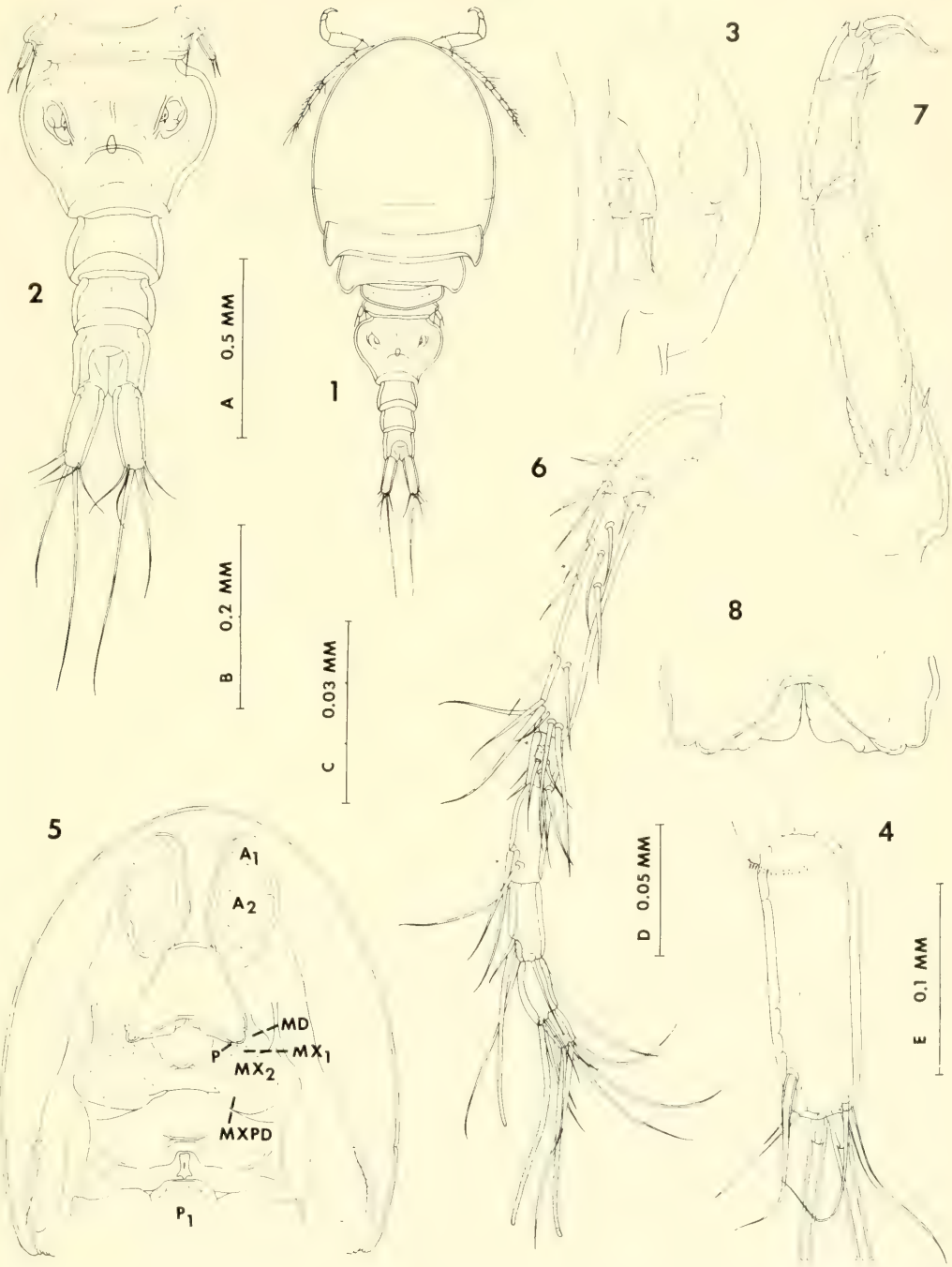
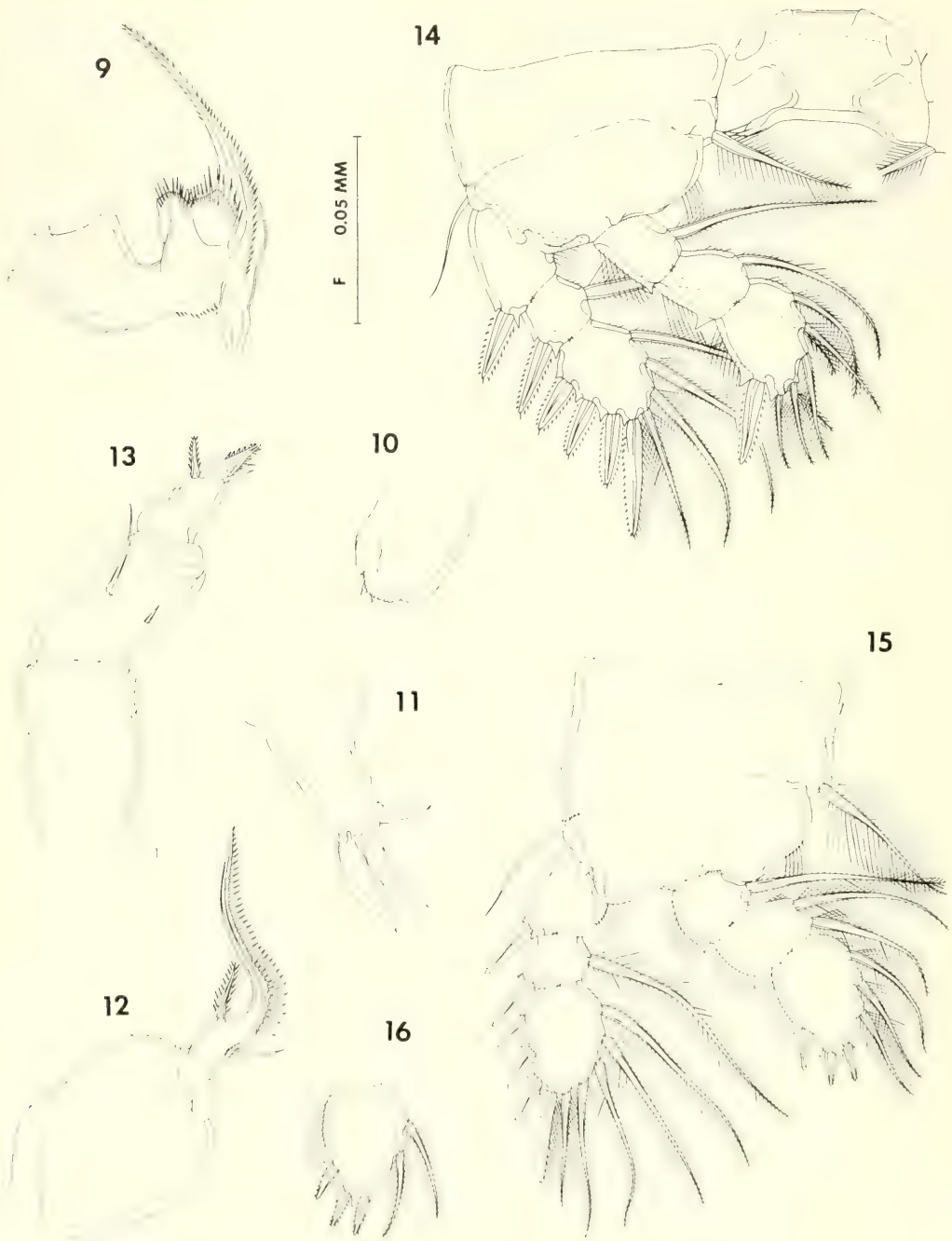
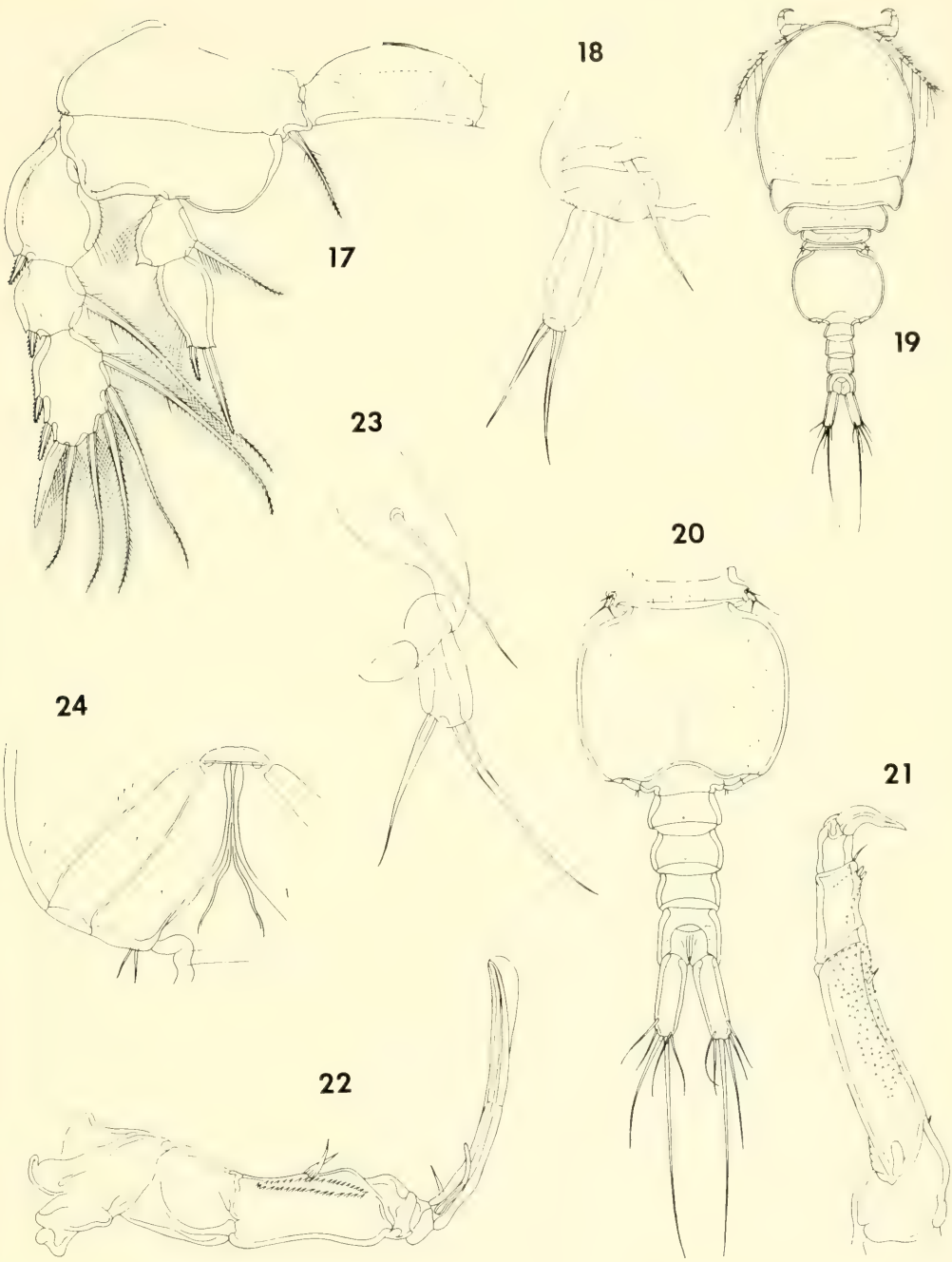


Figures 1–8. *Lichomolgus campulus* n. sp., female. 1, body, dorsal (A); 2, urosome, dorsal (B); 3, area of attachment of egg sac, dorsal (C); 4, caudal ramus, dorsal (D); 5, cephalosome, ventral (B); 6, first antenna, with arrows indicating positions of aesthetes in male, anterodorsal (E); 7, second antenna, outer (E); 8, labrum, ventral (E).

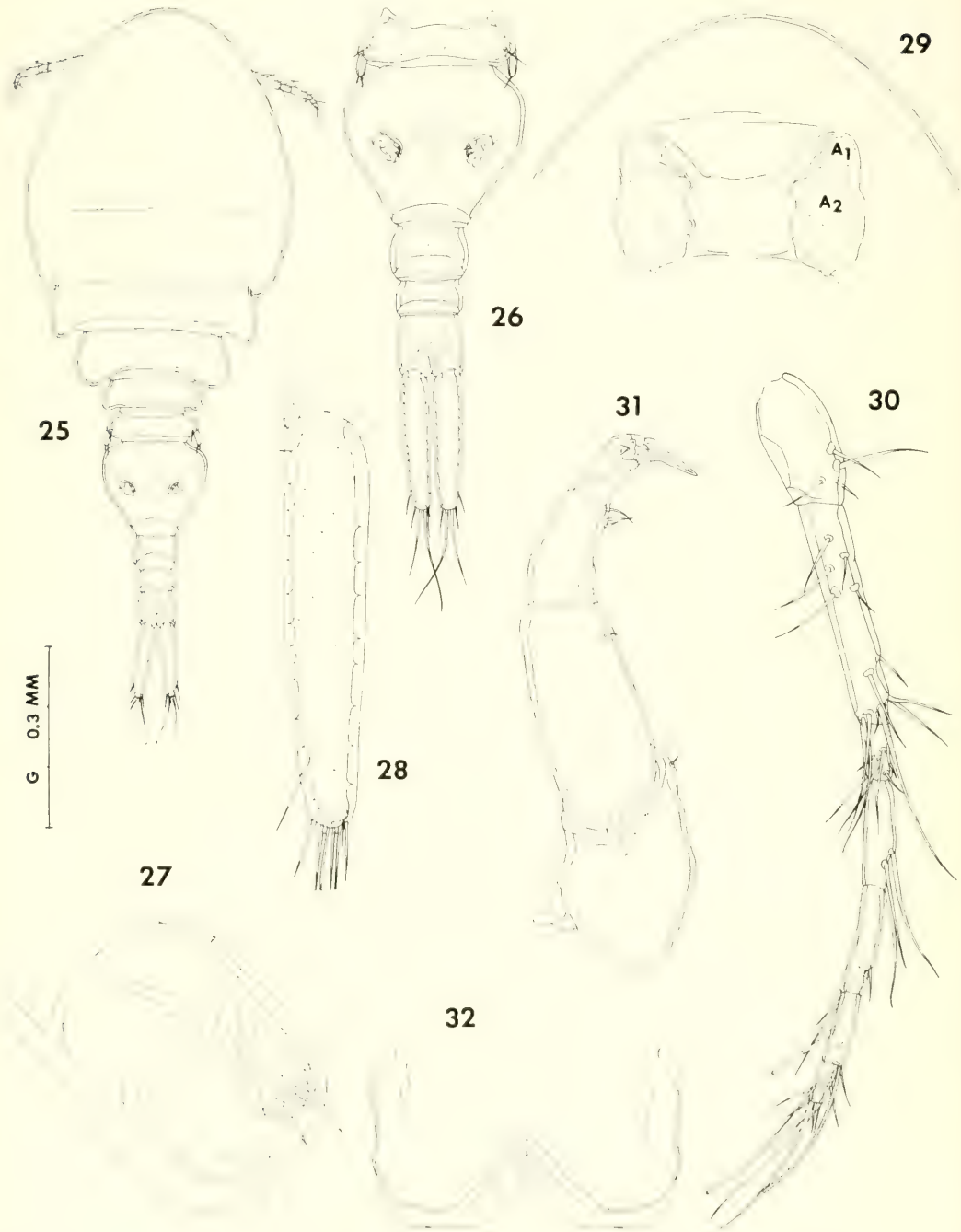


Figures 9–16. *Lichomolgus campulus* n. sp., female (continued). 9, mandible, posterior (F); 10, paragnath, anterior (F); 11, first maxilla, anterior (F); 12, second maxilla, posterior (D); 13, maxilliped, inner (F); 14, leg 1 and intercoxal plate, anterior (D); 15, leg 2, anterior (D); 16, last segment of endopod of leg 3, anterior (D).

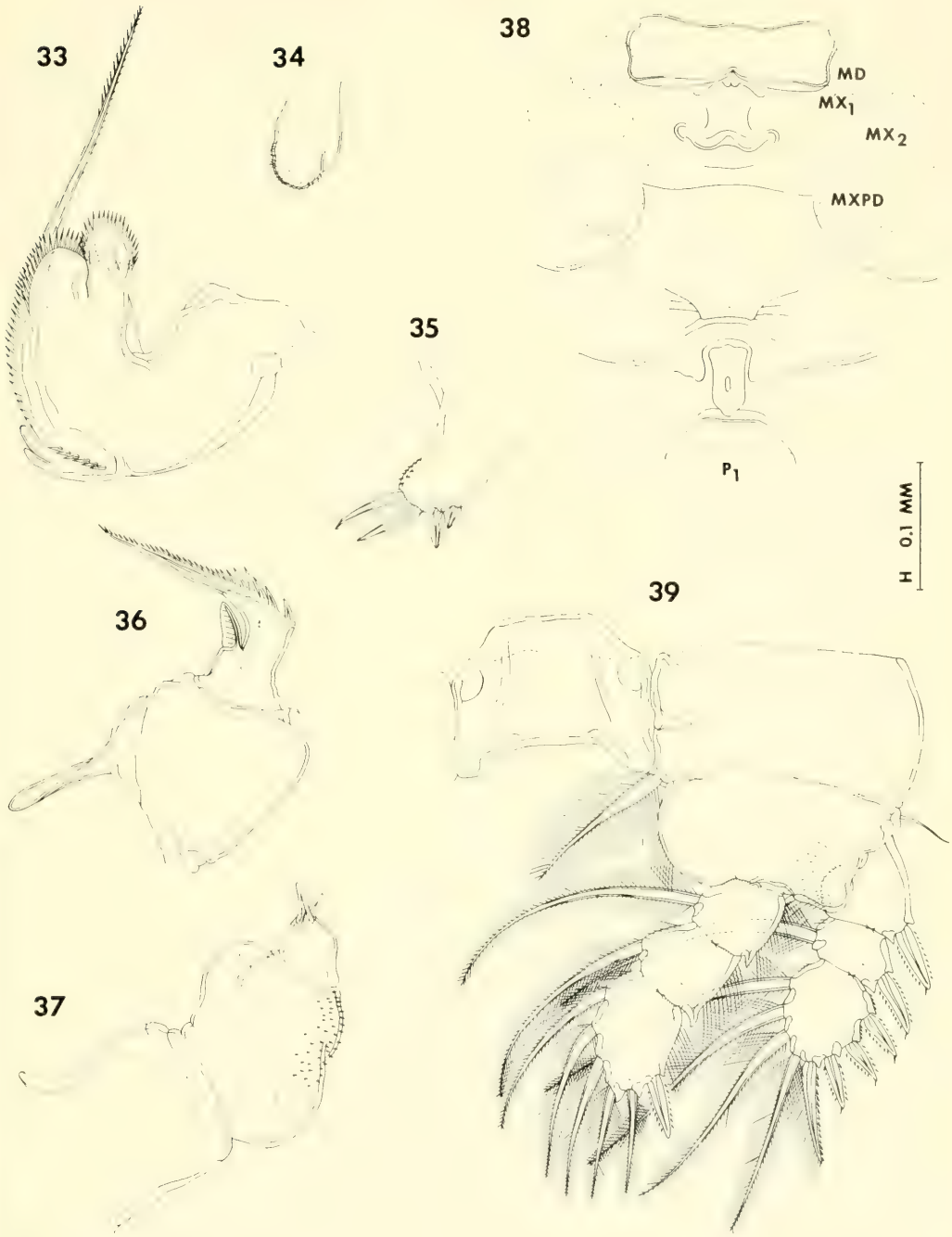


Figures 17–18. *Lichomolgus campulus* n. sp., female (continued). 17, leg 4 and intercoxal plate, anterior (D); 18, leg 5, dorsal (F).

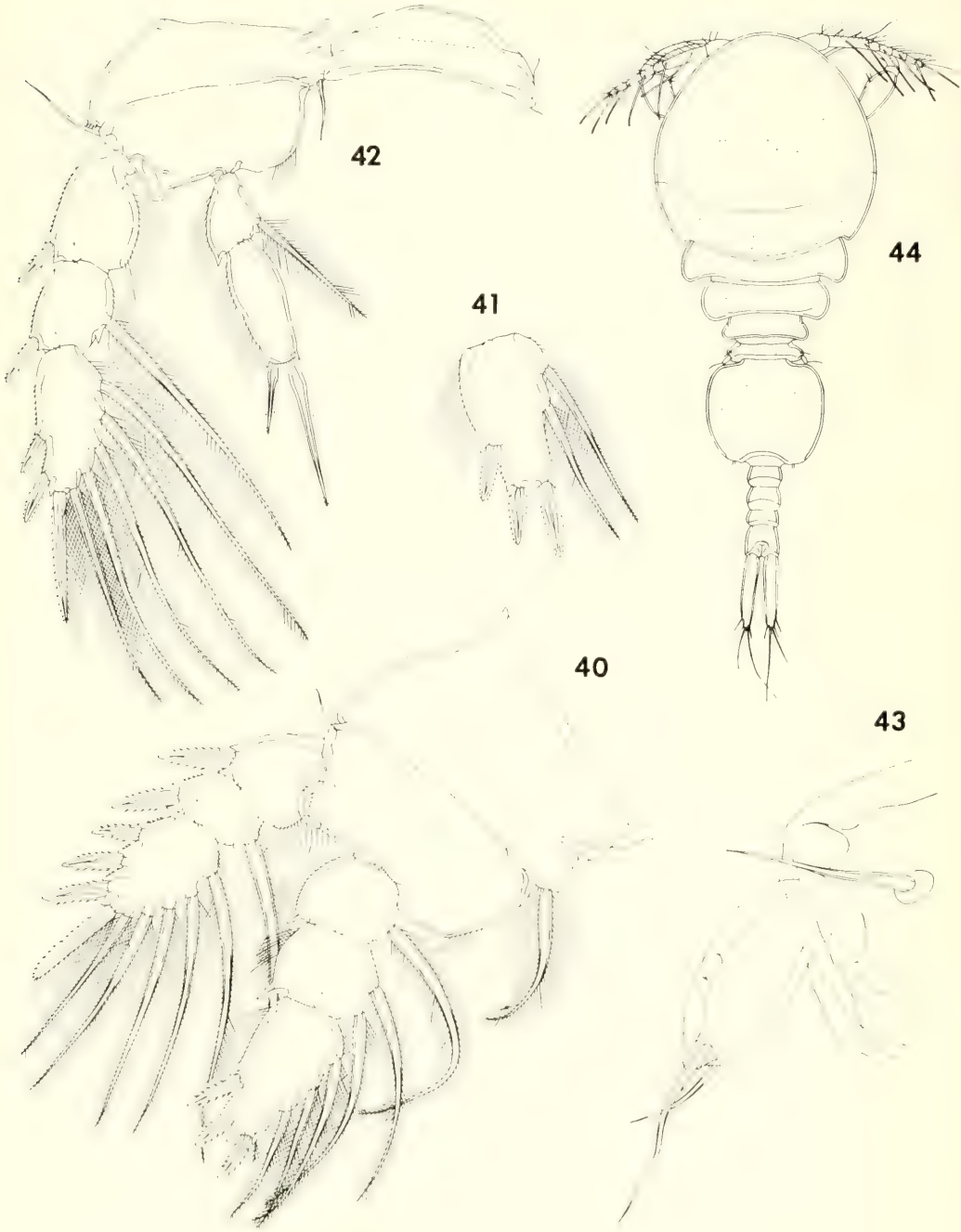
Figures 19–24. *Lichomolgus campulus* n. sp., male. 19, body, dorsal (A); 20, urosome, dorsal (B); 21, second antenna, outer (E); 22, maxilliped, inner (E); 23, leg 5, posterodorsal (G); 24, leg 6, ventral (E).



Figures 25–32. *Lichomolgus digitatus* n. sp., female. 25, body, dorsal (A); 26, urosome, dorsal (G); 27, area of attachment of egg sac, dorsal (C); 28, caudal ramus, dorsal (E); 29, rostral area, ventral (B); 30, first antenna, anterodorsal (E); 31, second antenna, outer (E); 32, labrum, ventral (E).

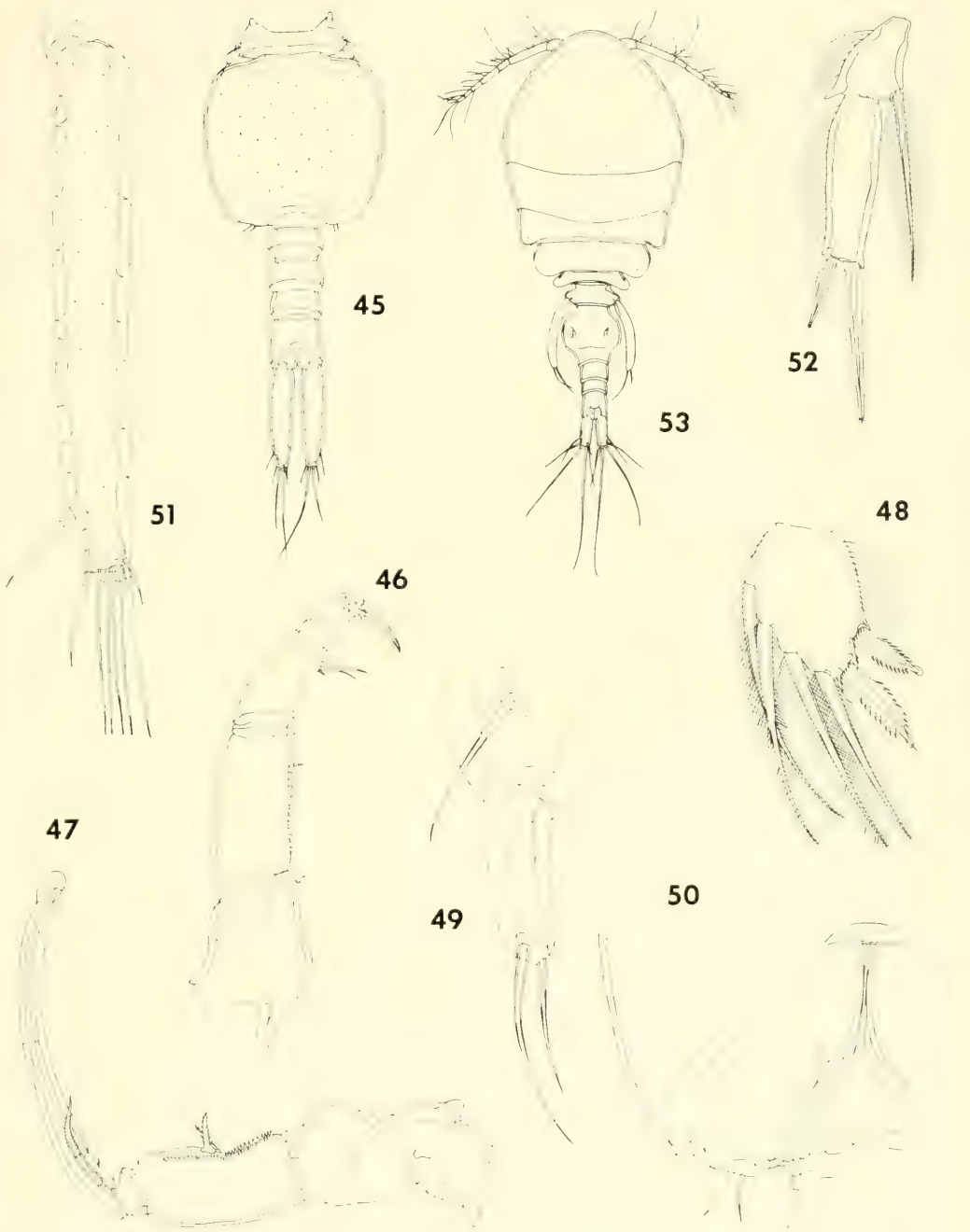


Figures 33–39. *Lichomolgus digitatus* n. sp., female (continued). 33, mandible, posterior (D); 34, paragnath, ventral (D); 35, first maxilla, ventral (D); 36, second maxilla, posterior (E); 37, maxilliped, anterior (D); 38, oral and postoral areas, with edge of labrum turned ventrally, ventral (H); 39, leg 1 and intercoxal plate, anterior (E).



Figures 40–43. *Lichomolgus digitatus* n. sp., female (continued). 40, leg 2, anterior (E); 41, last segment of endopod of leg 3, anterior (E); 42, leg 4 and intercoxal plate, anterior (E); 43, leg 5, dorsal (C).

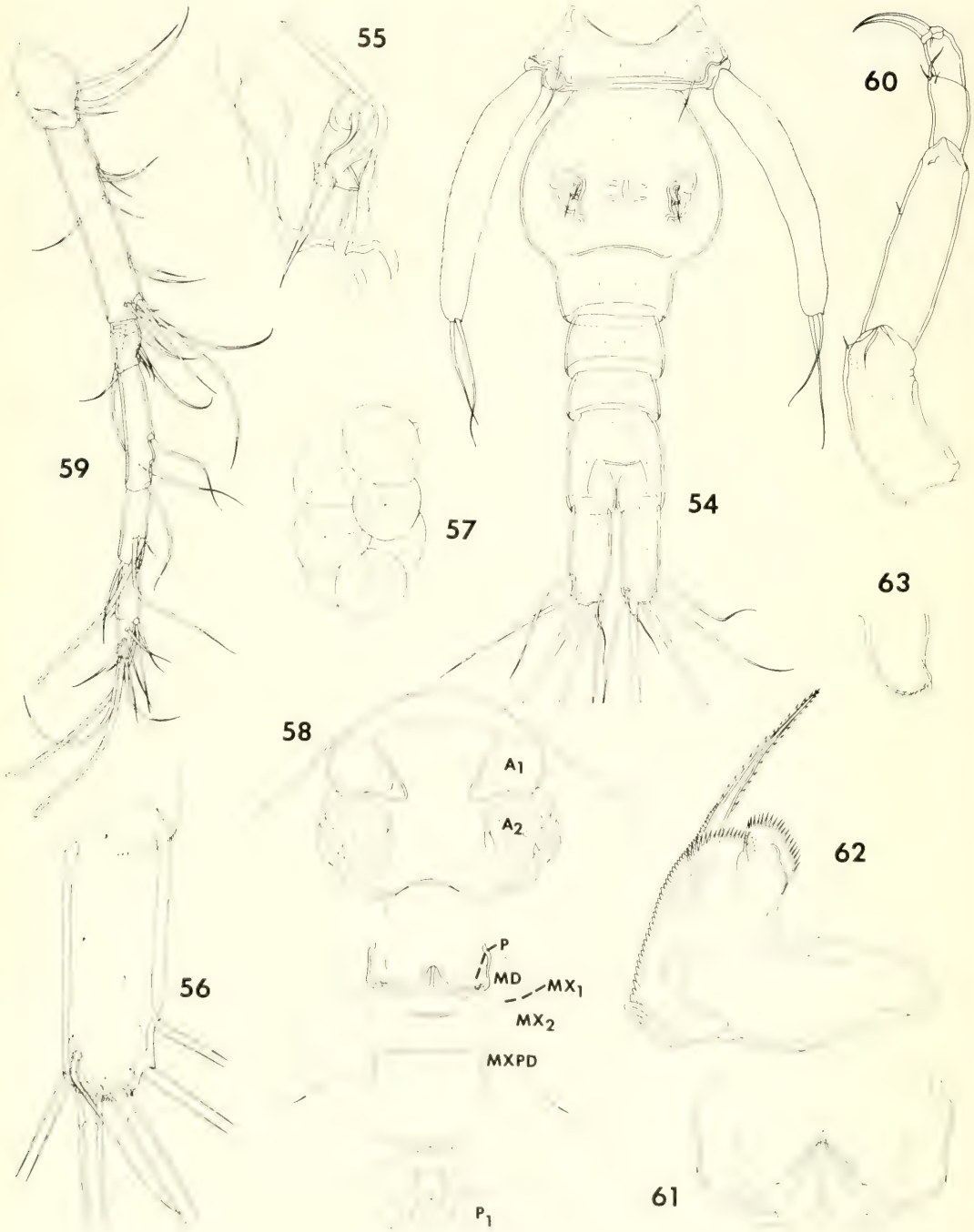
Figure 44. *Lichomolgus digitatus* n. sp., male. 44, body, dorsal (A).



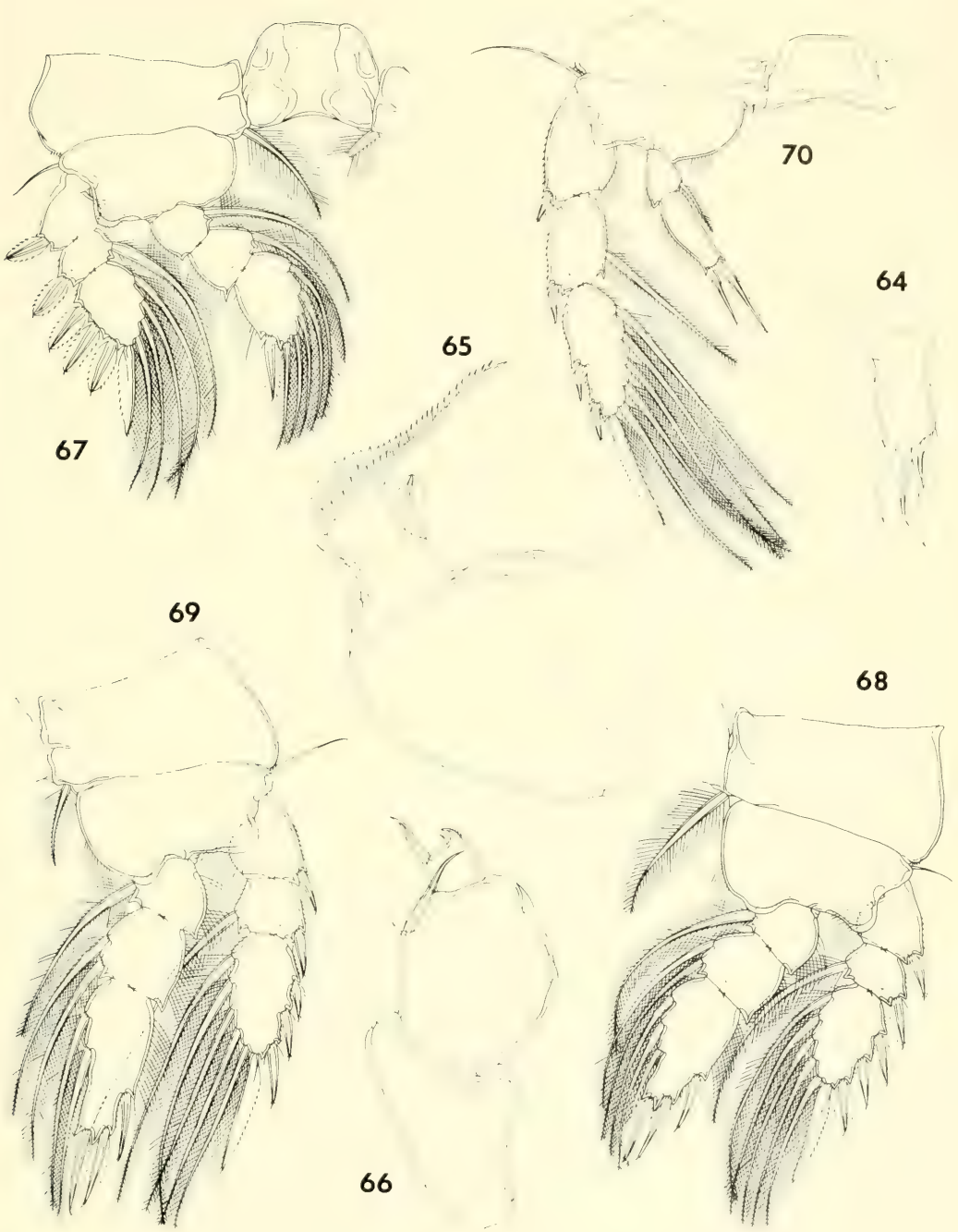
Figures 45–50. *Lichomolgus digitatus* n. sp., male (continued). 45, urosome, dorsal (G); 46, second antenna, inner (E); 47, maxilliped, inner (H); 48, last segment of endopod of leg 1, anterior (D); 49, leg 5, dorsal (C); 50, leg 6, ventral (E).

Figures 51–52. *Lichomolgus digitatus* n. sp., female, from *Porites*. 51, caudal ramus, dorsal (E); 52, endopod of leg 4, anterior (E).

Figure 53. *Lichomolgus prolixipes* n. sp., female. 53, body, dorsal (A).



Figures 54–63. *Lichomolgus prolixipes* n. sp., female (continued). 54, urosome, dorsal (G); 55, area of attachment of egg sac, dorsal (C); 56, caudal ramus, dorsal (F); 57, egg sac, lateral (G); 58, rostral, oral, and postoral areas, ventral (H); 59, first antenna, posteroventral (E); 60, second antenna, inner (E); 61, labrum, ventral (D); 62, mandible, posterior (F); 63, paragnath, ventral (F).



Figures 64–70. *Lichomologus prolixipes* n. sp., female (continued). 64, first maxilla, anterior (F); 65, second maxilla, posterior (F); 66, maxilliped, posterointernal (F); 67, leg 1 and intercoxal plate, anterior (E); 68, leg 2, anterior (E); 69, leg 3, anterior (E); 70, leg 4 and intercoxal plate, anterior (E).

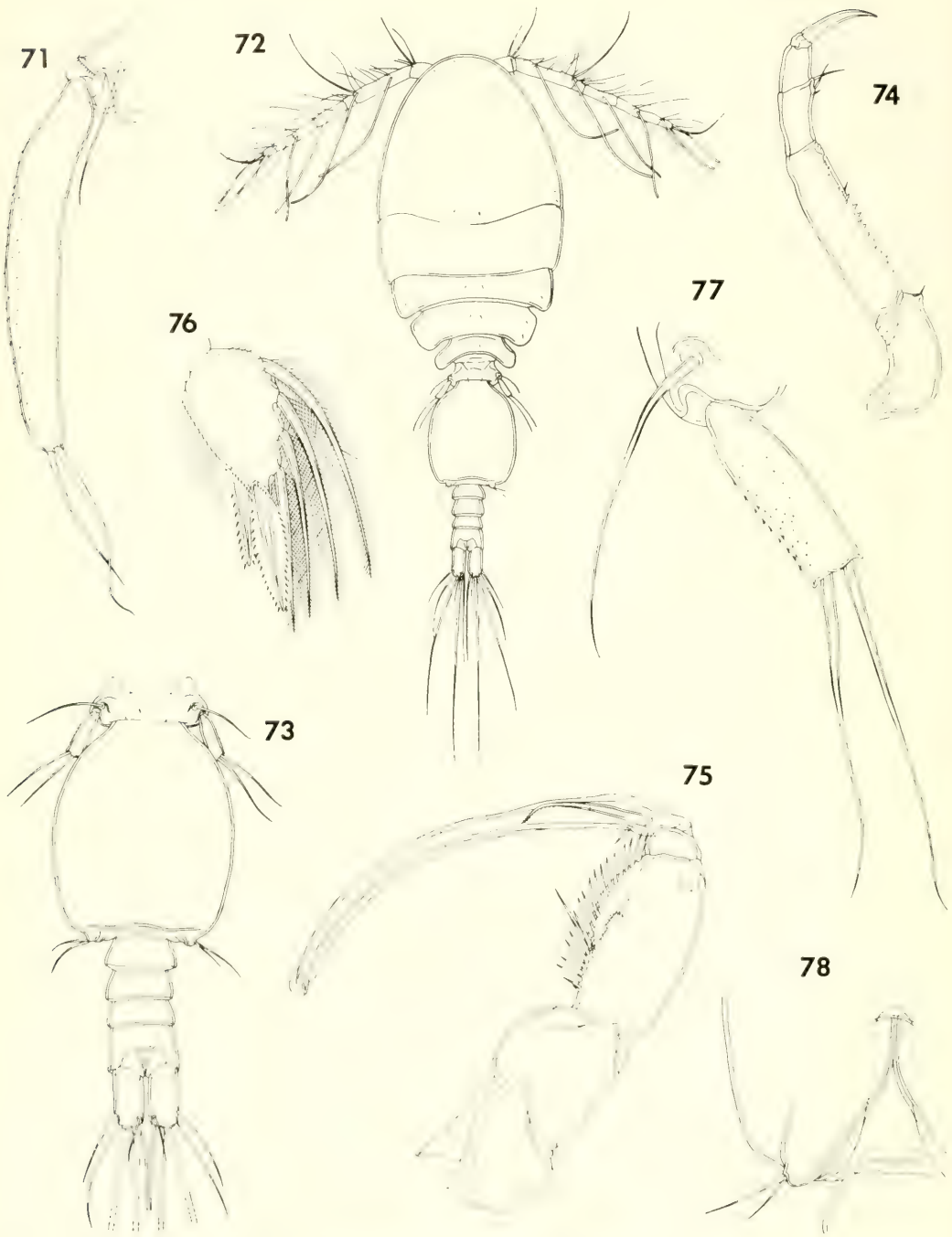
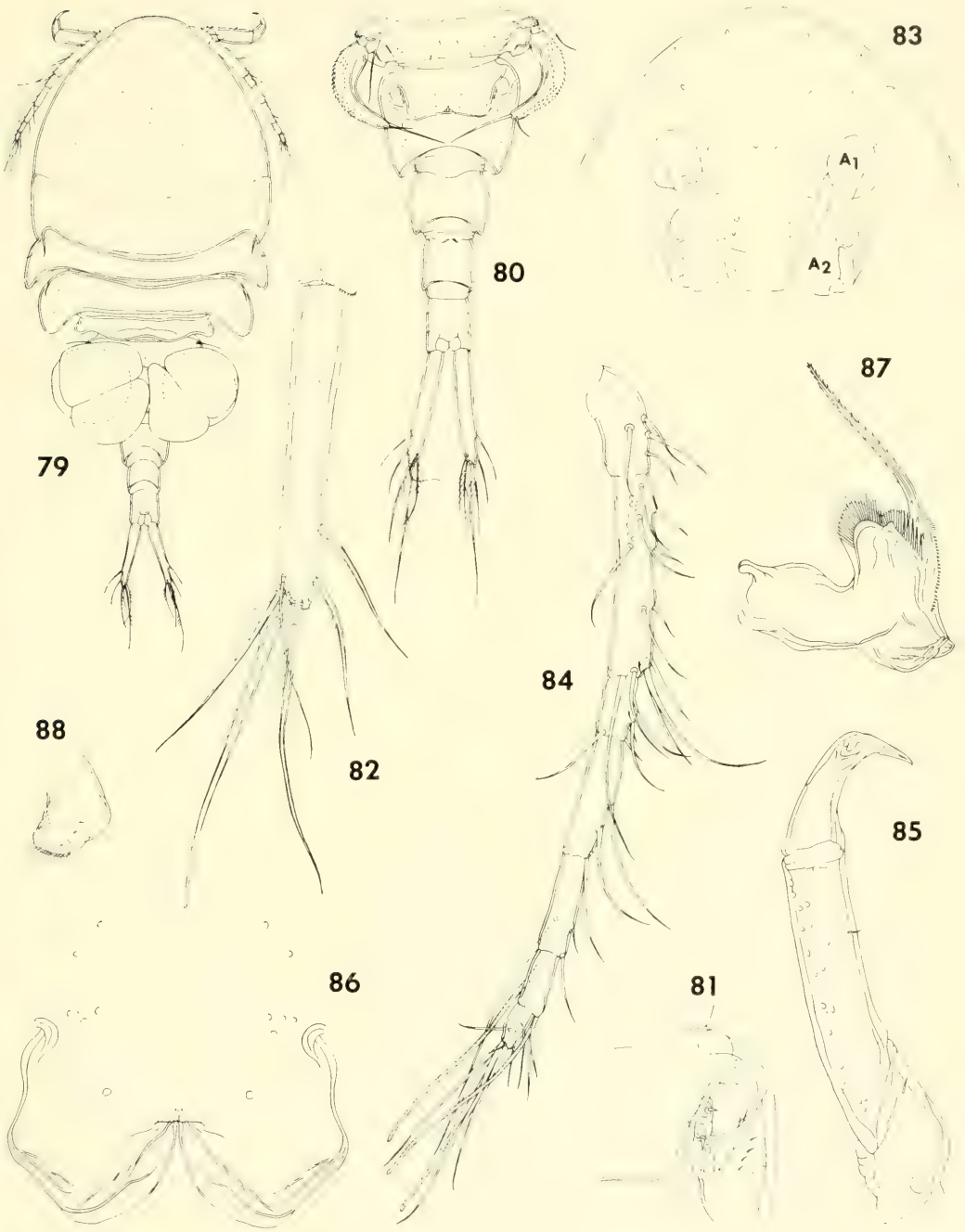
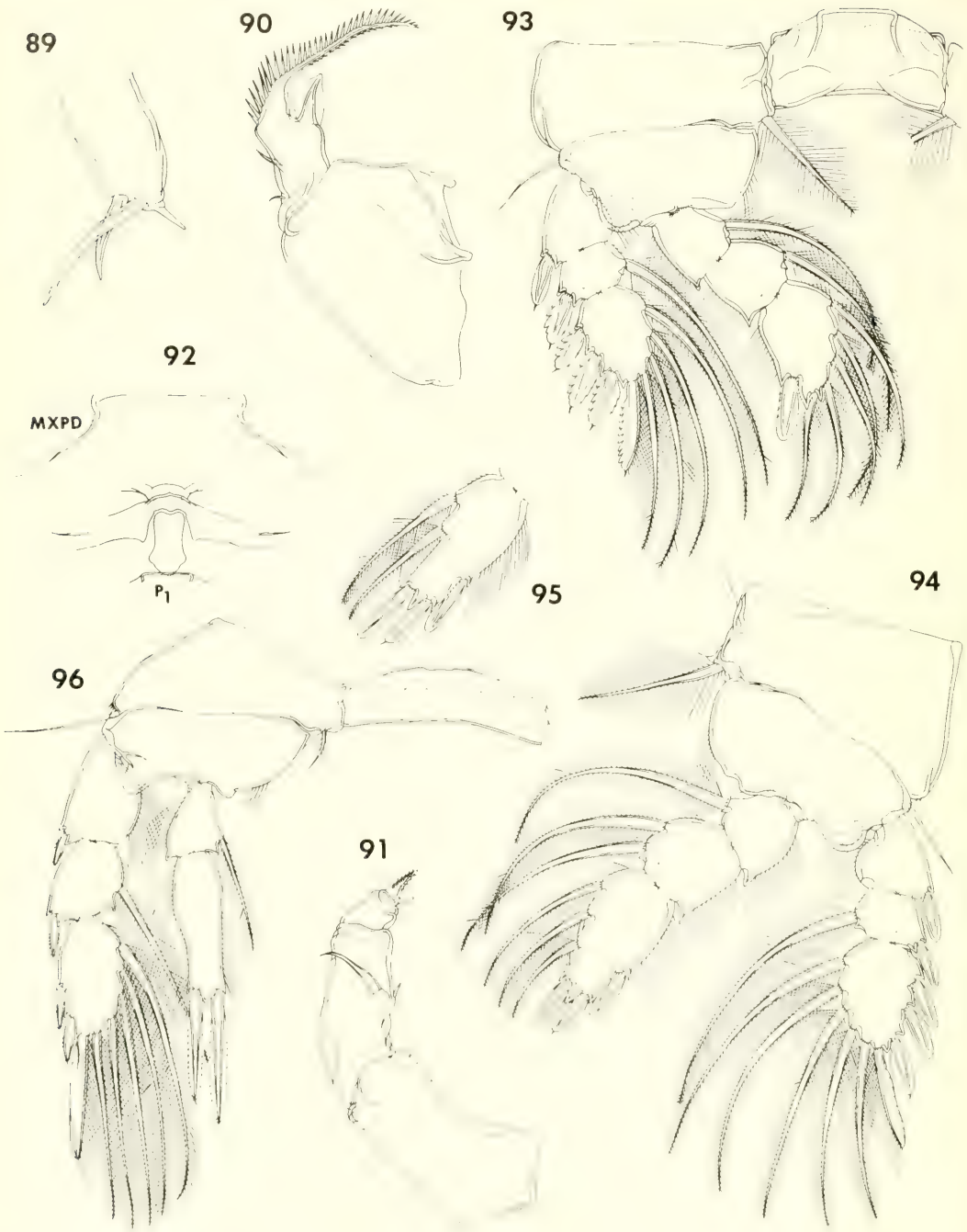


Figure 71. *Lichomolgus prolixipes* n. sp., female (continued). 71, leg 5, dorsal (E).

Figures 72–78. *Lichomolgus prolixipes* n. sp., male. 72, body, dorsal (G); 73, urosome, dorsal (H); 74, second antenna, inner (E); 75, maxilliped, inner (D); 76, last segment of endopod of leg 1, anterior (F); 77, leg 5, dorsal (C); 78, leg 6, ventral (D).



Figures 79–88. *Lichomolgus arcuatipes* n. sp., female. 79, body, dorsal (G); 80, urosome, dorsal (B); 81, area of attachment of egg sac, dorsal (D); 82, caudal ramus, dorsal (D); 83, rostral area, ventral (H); 84, first antenna, dorsal (D); 85, second antenna, outer (D); 86, labrum, ventral (F); 87, mandible, posterior (F); 88, paragnath, ventral (C).



Figures 89–96. *Lichomolgus arcuatipes* n. sp., female (continued). 89, first maxilla, posterior (C); 90, second maxilla, anterior (F); 91, maxilliped, posterior (F); 92, postoral area, ventral (E); 93, leg 1 and intercoxal plate, anterior (D); 94, leg 2, anterior (D); 95, last segment of endopod of leg 3, anterior (D); 96, leg 4 and intercoxal plate, anterior (D).

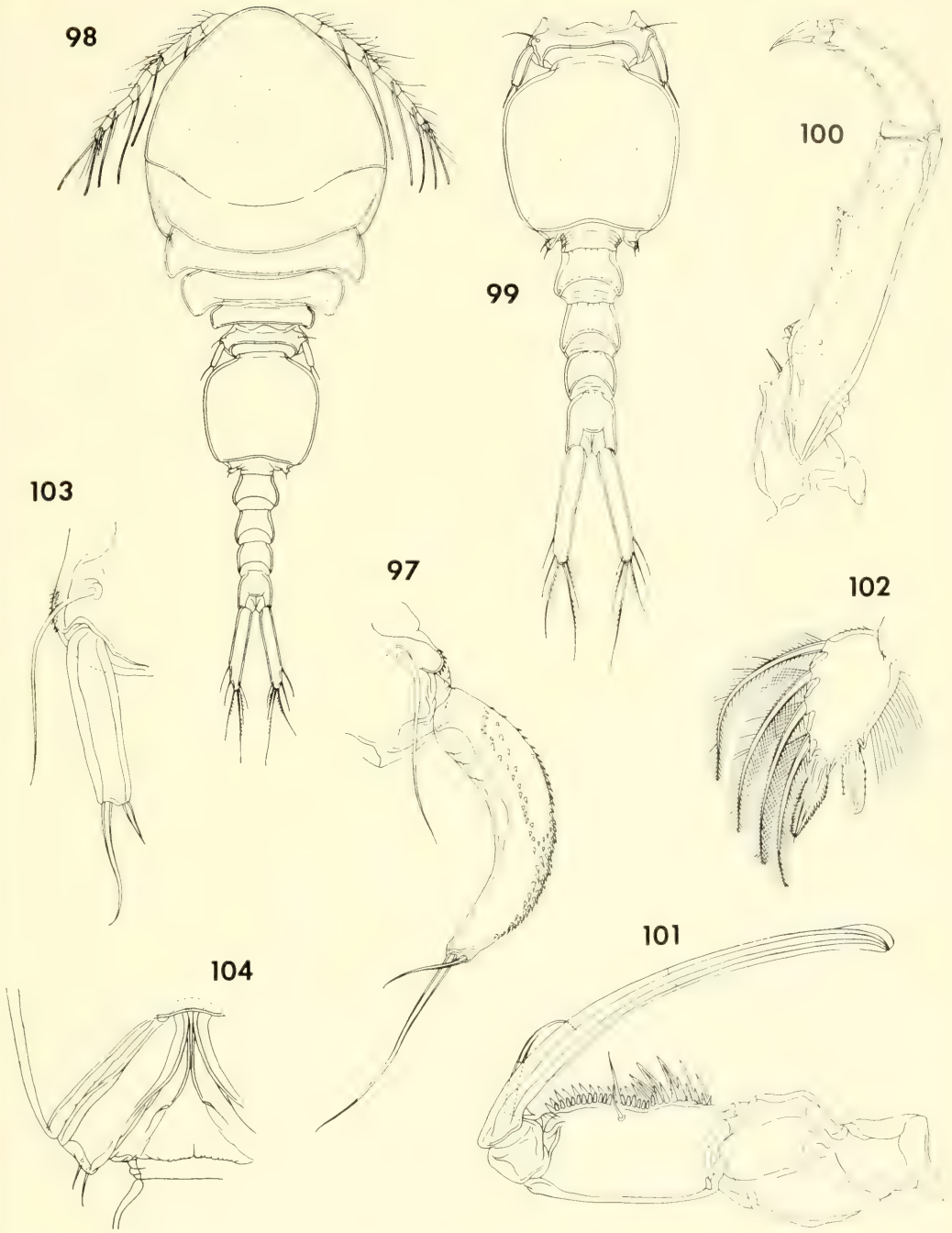
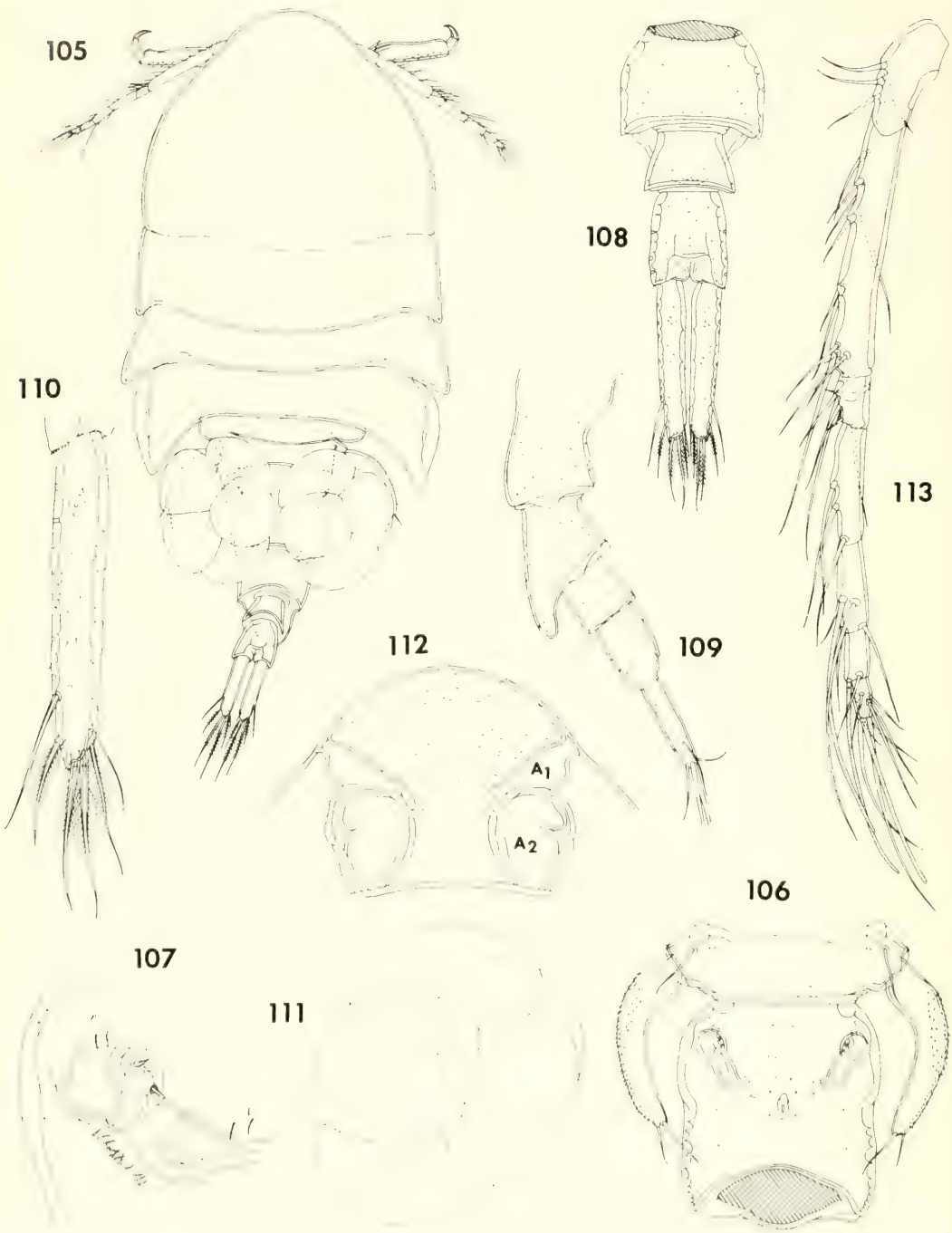
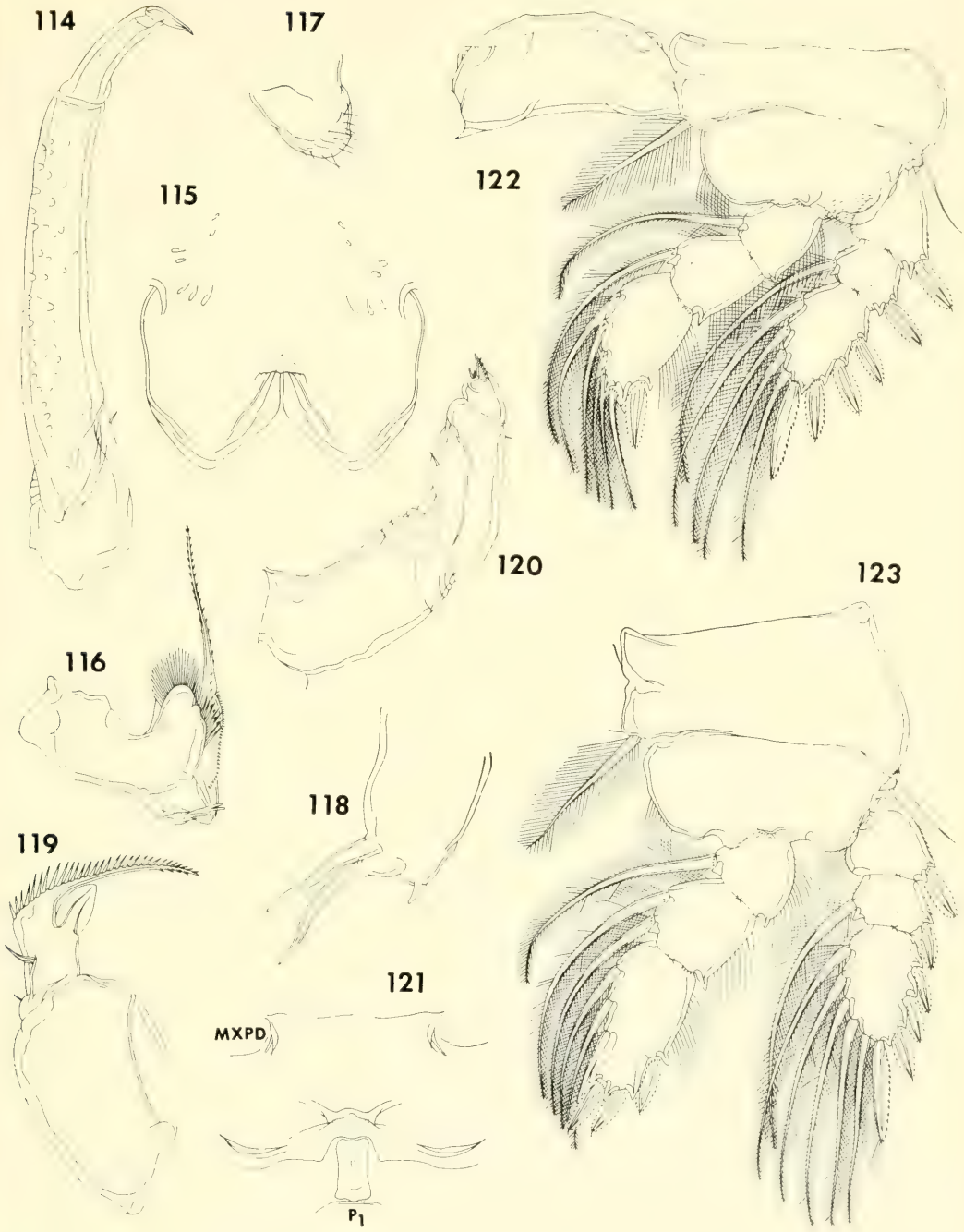


Figure 97. *Lichomolgus arcuatipes* n. sp., female (continued). 97, leg 5, dorsal (D).

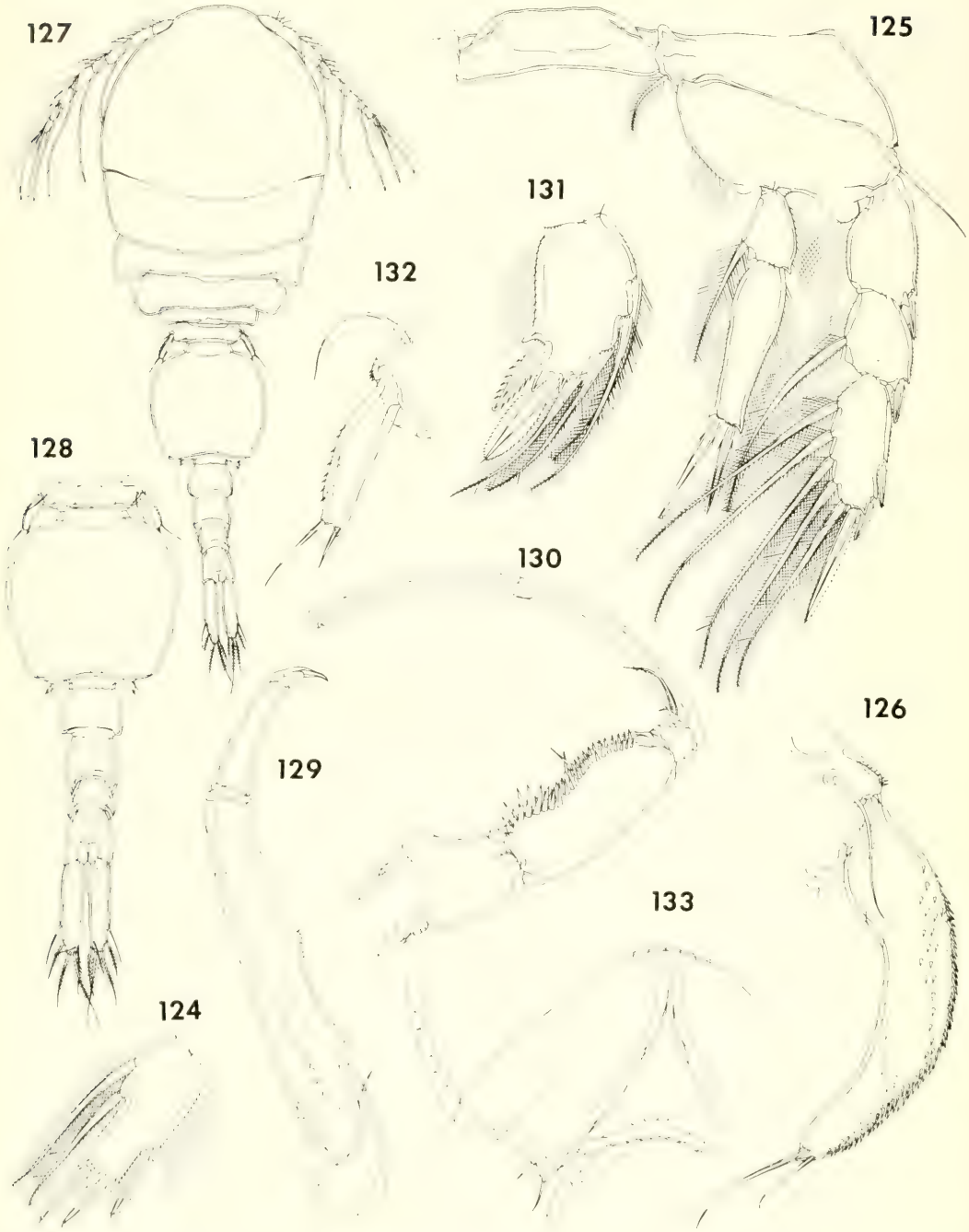
Figures 98–104. *Lichomolgus arcuatipes* n. sp., male. 98, body, dorsal (G); 99, urosome, dorsal (B); 100, second antenna, outer (D); 101, maxilliped, outer (E); 102, last segment of endopod of leg 1, anterior (D); 103, leg 5, dorsal (F); 104, leg 6, ventral (E).



Figures 105–113. *Lichomolgus lobophorus* n. sp., female. 105, body, dorsal (G); 106, segment of leg 5 and genital segment, dorsal (B); 107, area of attachment of egg sac, dorsolateral (D); 108, postgenital segments and caudal rami, dorsal (B); 109, part of urosome, lateral (B); 110, caudal ramus, dorsal (E); 111, egg sac, dorsal (H); 112, rostral area, ventral (H); 113, first antenna, ventral (E).

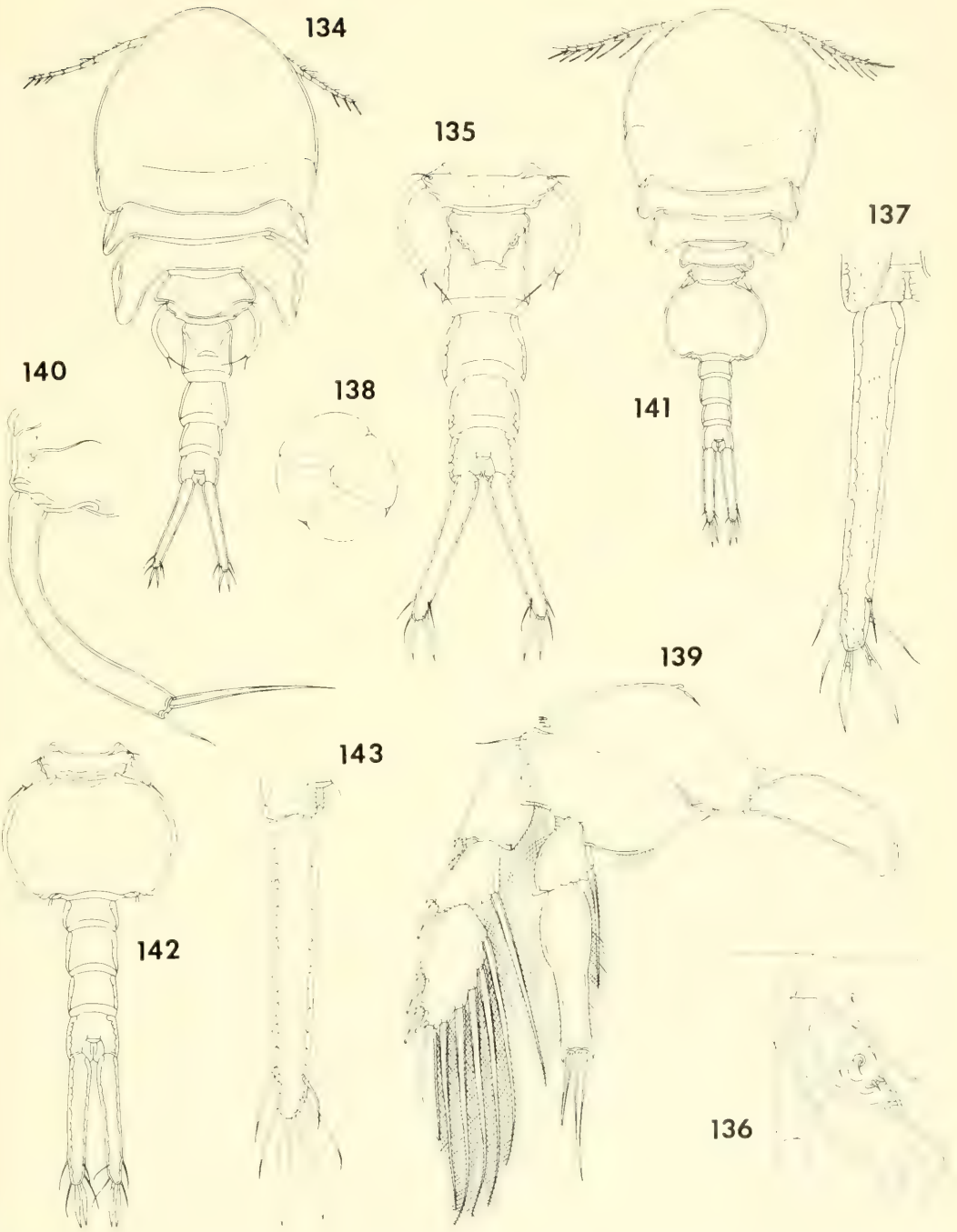


Figures 114–123. *Lichomolgus lobophorus* n. sp., female (continued). 114, second antenna, outer (E); 115, labrum, ventral (D); 116, mandible, posterior (D); 117, paragnath, ventral (C); 118, first maxilla, posterior (C); 119, second maxilla, posterior, (D); 120, maxilliped, anterior (D); 121, postoral area, ventral (H); 122, leg 1 and intercoxal plate, anterior (E); 123, leg 2, anterior (E).



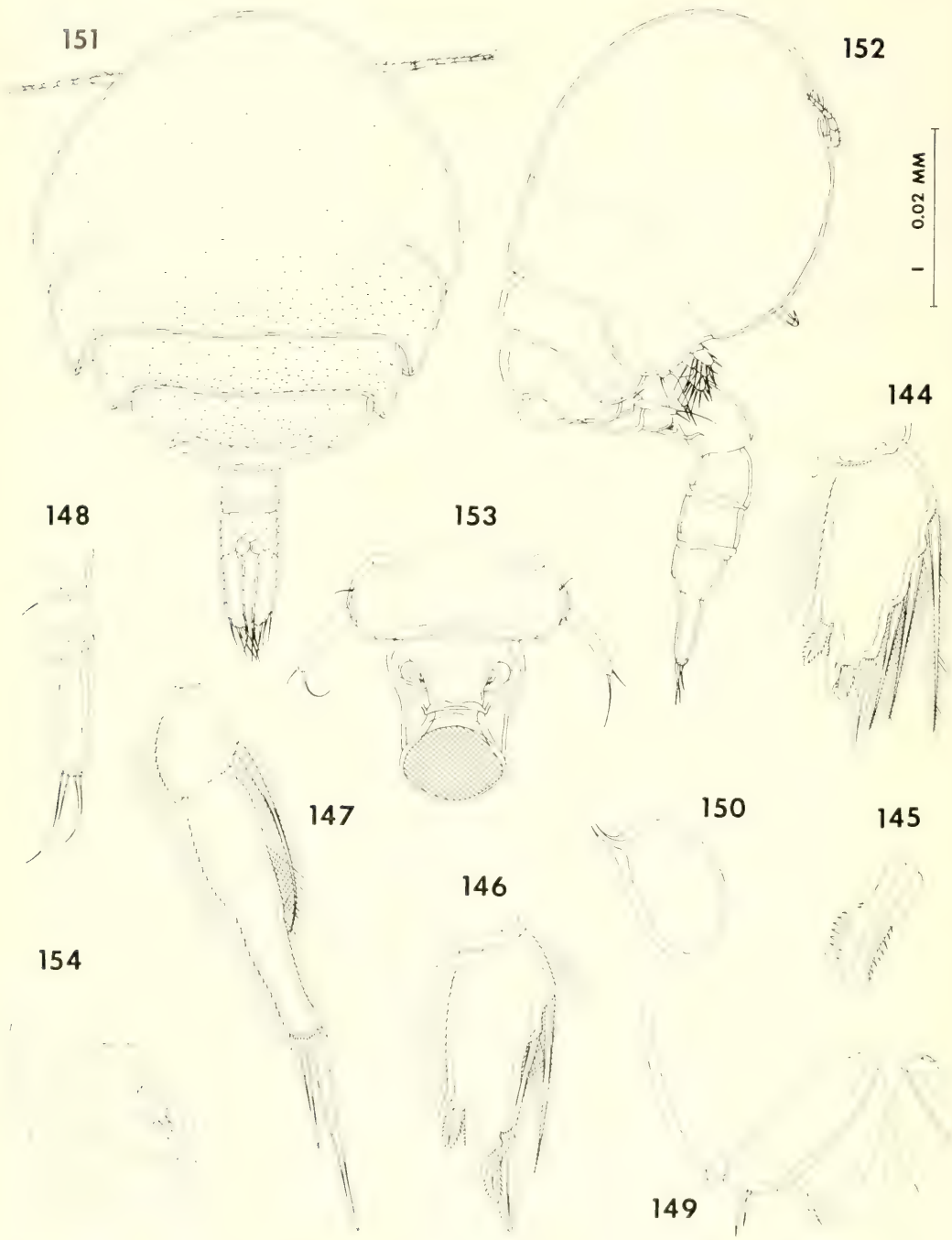
Figures 124–126. *Lichomolgus lobophorus* n. sp., female (continued). 124, last segment of endopod of leg 3, anterior (E); 125, leg 4 and intercoxal plate, anterior (E); 126, leg 5, dorsal (E).

Figures 127–133. *Lichomolgus lobophorus* n. sp., male. 127, body, dorsal (G); 128, urosome, dorsal (B); 129, second antenna, outer (E); 130, maxilliped, inner (H); 131, last segment of endopod of leg 1, anterior (D); 132, leg 5, dorsal (D); 133, leg 6, ventral (E)



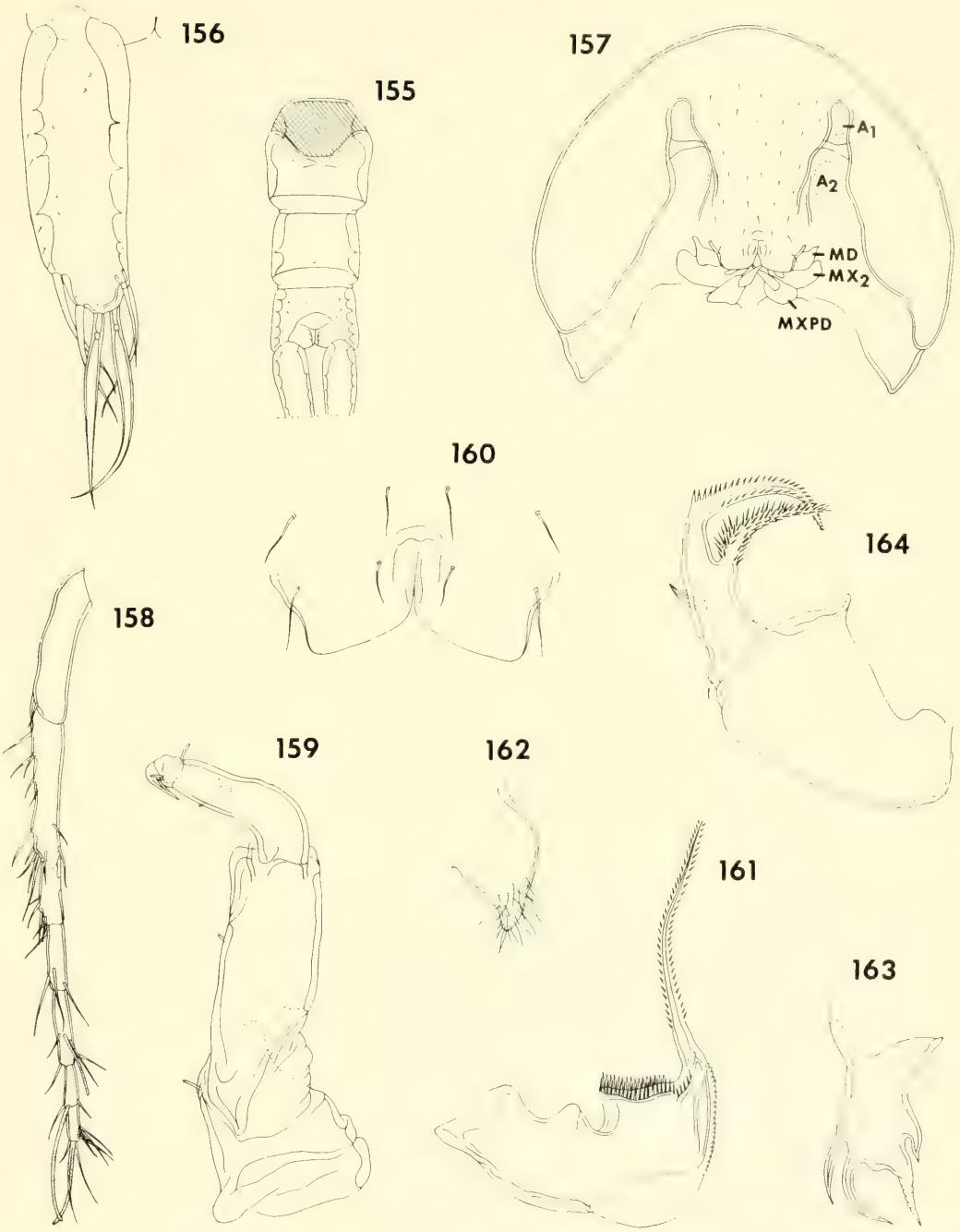
Figures 134–140. *Lichomolgus geminus* n. sp., female. 134, body, dorsal (A); 135, urosome, dorsal (G); 136, area of attachment of egg sac, dorsal (F); 137, caudal ramus, dorsal (H); 138, egg sac, dorsal (G); 139, leg 4 and intercoxal plate, anterior (E); 140, leg 5, dorsal (E).

Figures 141–143. *Lichomolgus geminus* n. sp., male. 141, body, dorsal (A); 142, urosome, dorsal (G); 143, caudal ramus, dorsal (H).

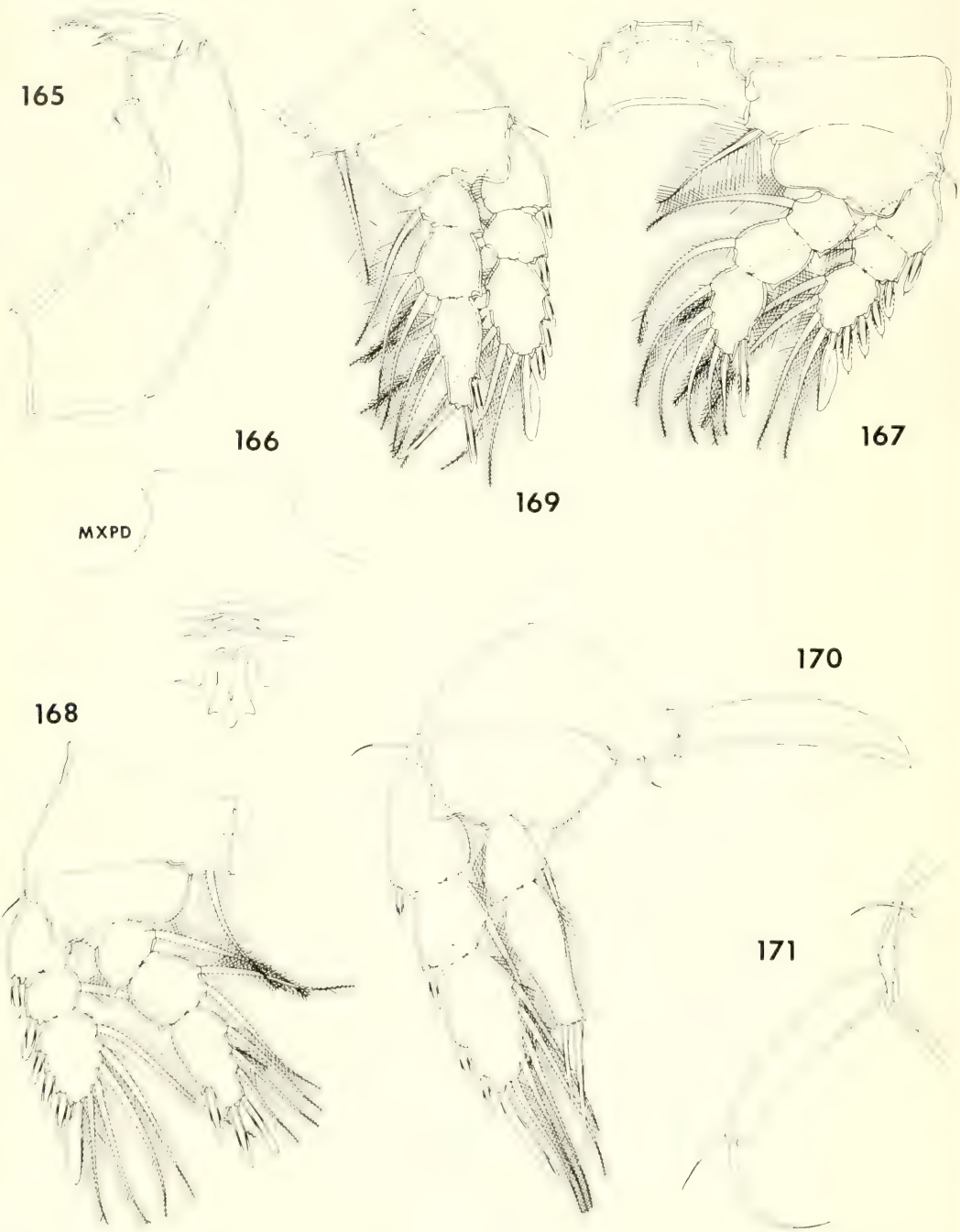


Figures 144–150. *Lichomolgus geminus* n. sp., male (continued). 144, last segment of endopod of leg 2, anterior (D); 145, middle distal spine on last segment of endopod of leg 2, anterior (I); 146, last segment of endopod of leg 3, anterior (D); 147, endopod of leg 4, anterior (D); 148, leg 5, dorsal (D); 149, leg 6, ventral (E); 150, spermatophore, attached to female, dorsal (B).

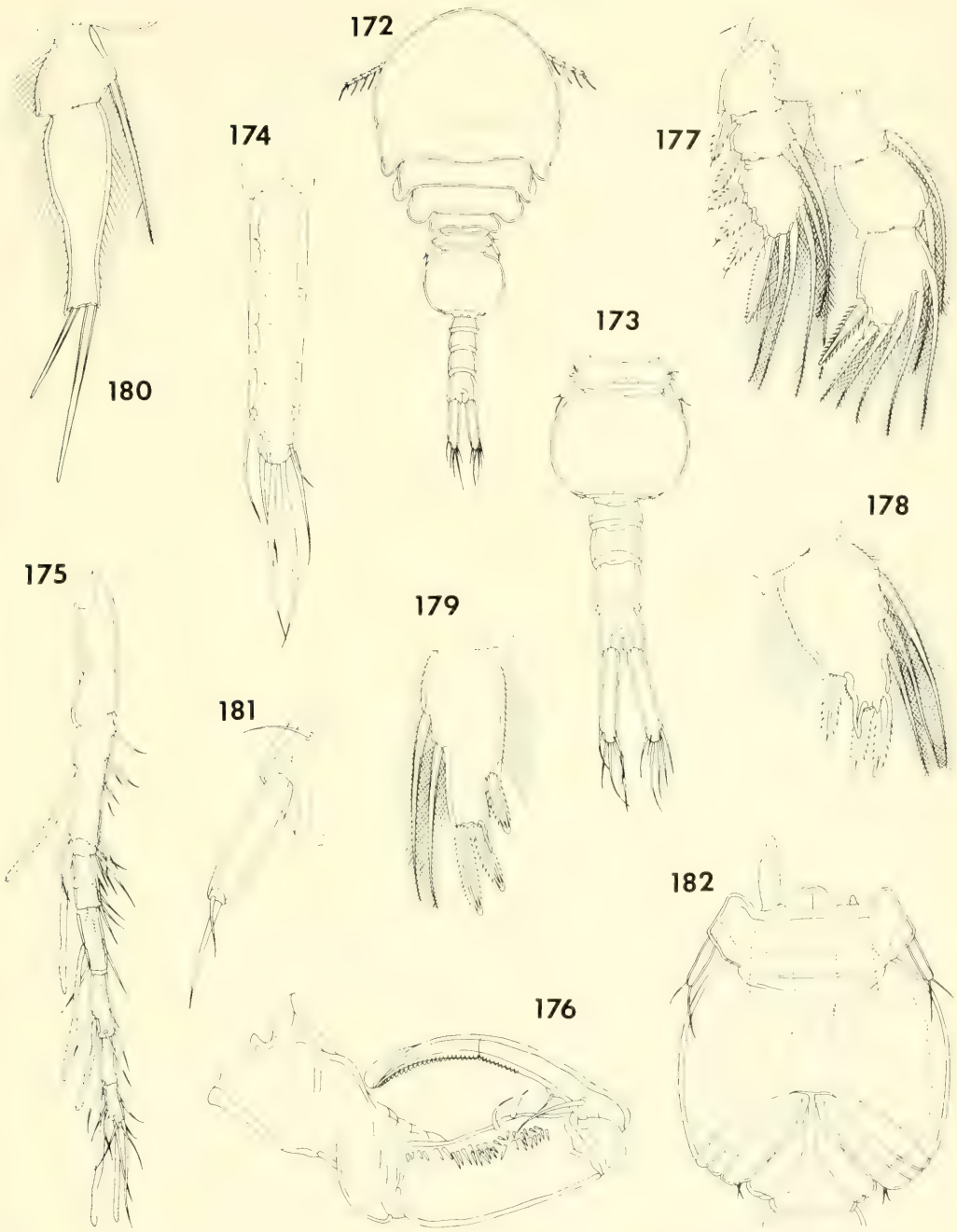
Figures 151–154. *Lichomolgus crassus* n. sp., female. 151, body, dorsal (G); 152, body, lateral (G); 153, segment of leg 5 and genital segment, dorsal (B); 154, area of attachment of egg sac, dorsal (F).



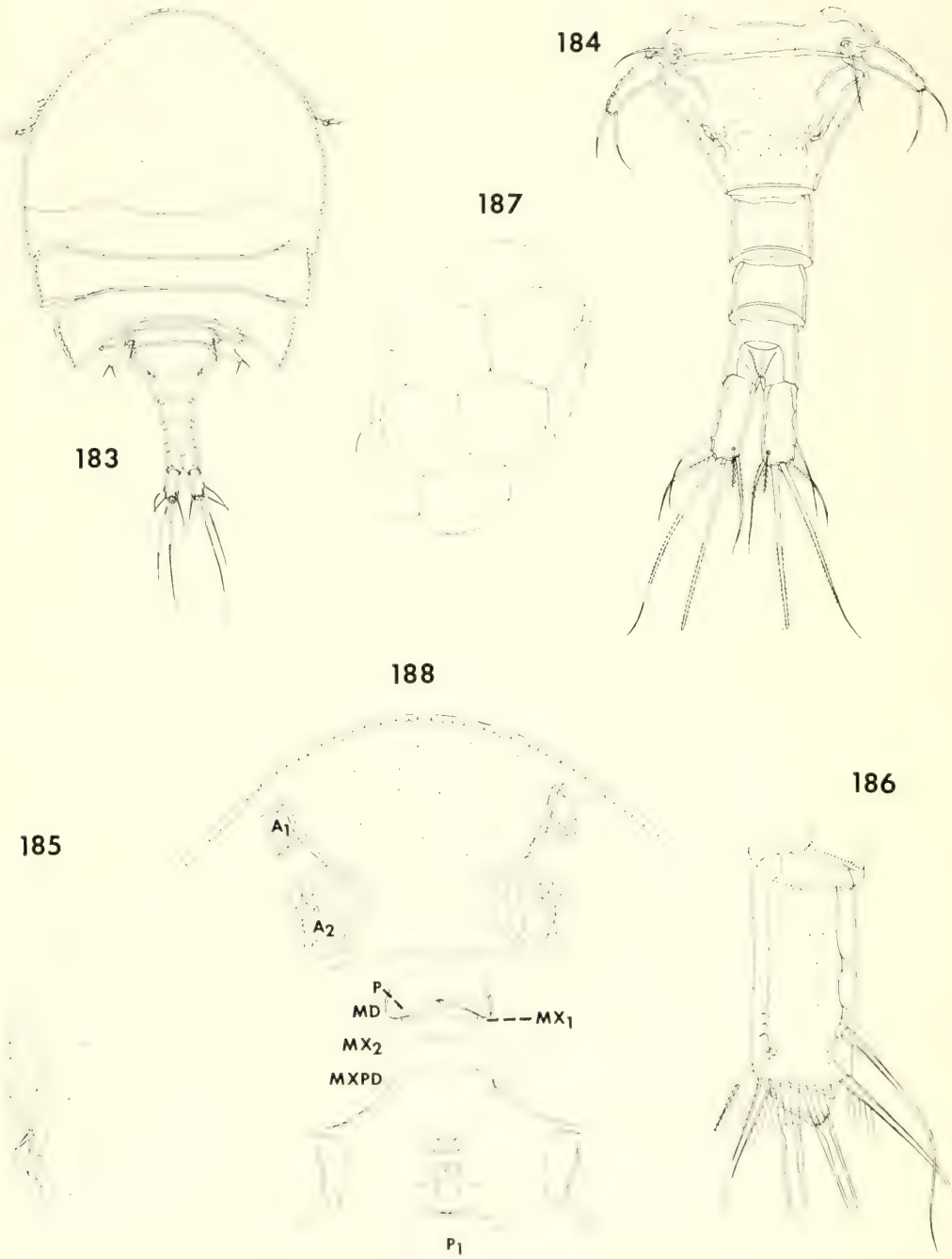
Figures 155–164. *Lichomolgus crassus* n. sp., female (continued). 155, postgenital segments, dorsal (B); 156, caudal ramus, dorsal (D); 157, anterior part of cephalosome, ventral (G); 158, first antenna, dorsal (E); 159, second antenna, outer (E); 160, labrum, ventral (E); 161, mandible, posterior (D); 162, paragnath, posterior (C); 163, first maxilla, anterior (D); 164, second maxilla, anterior (D).



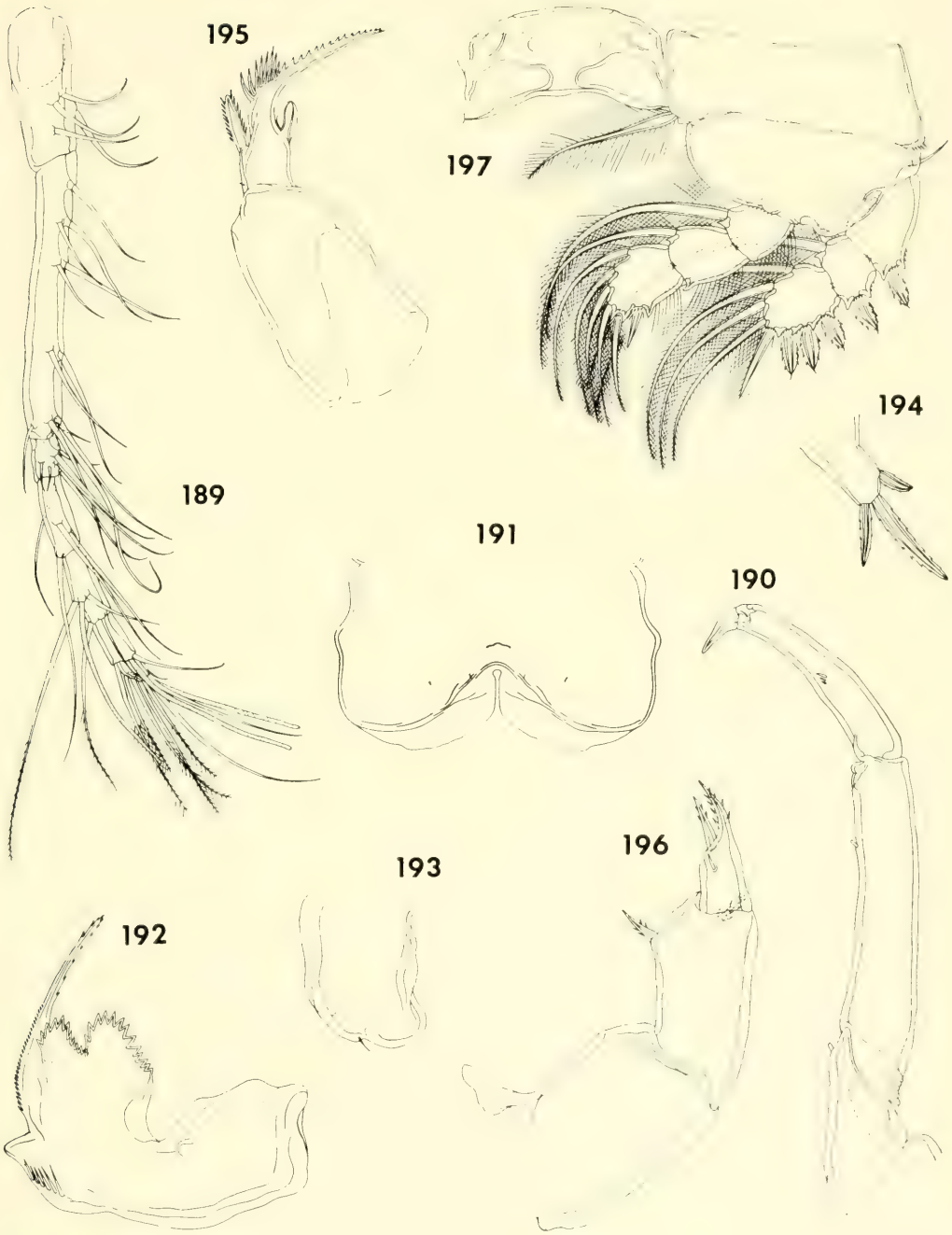
Figures 165–171. *Lichomologus crassus* n. sp., female (continued). 165, maxilliped, inner (D); 166, postoral area, ventral (E); 167, leg 1 and intercoxal plate, anterior (E); 168, leg 2, anterior (E); 169, leg 3, anterior (E); 170, leg 4 and intercoxal plate, anterior (D); 171, leg 5, dorsal (D).



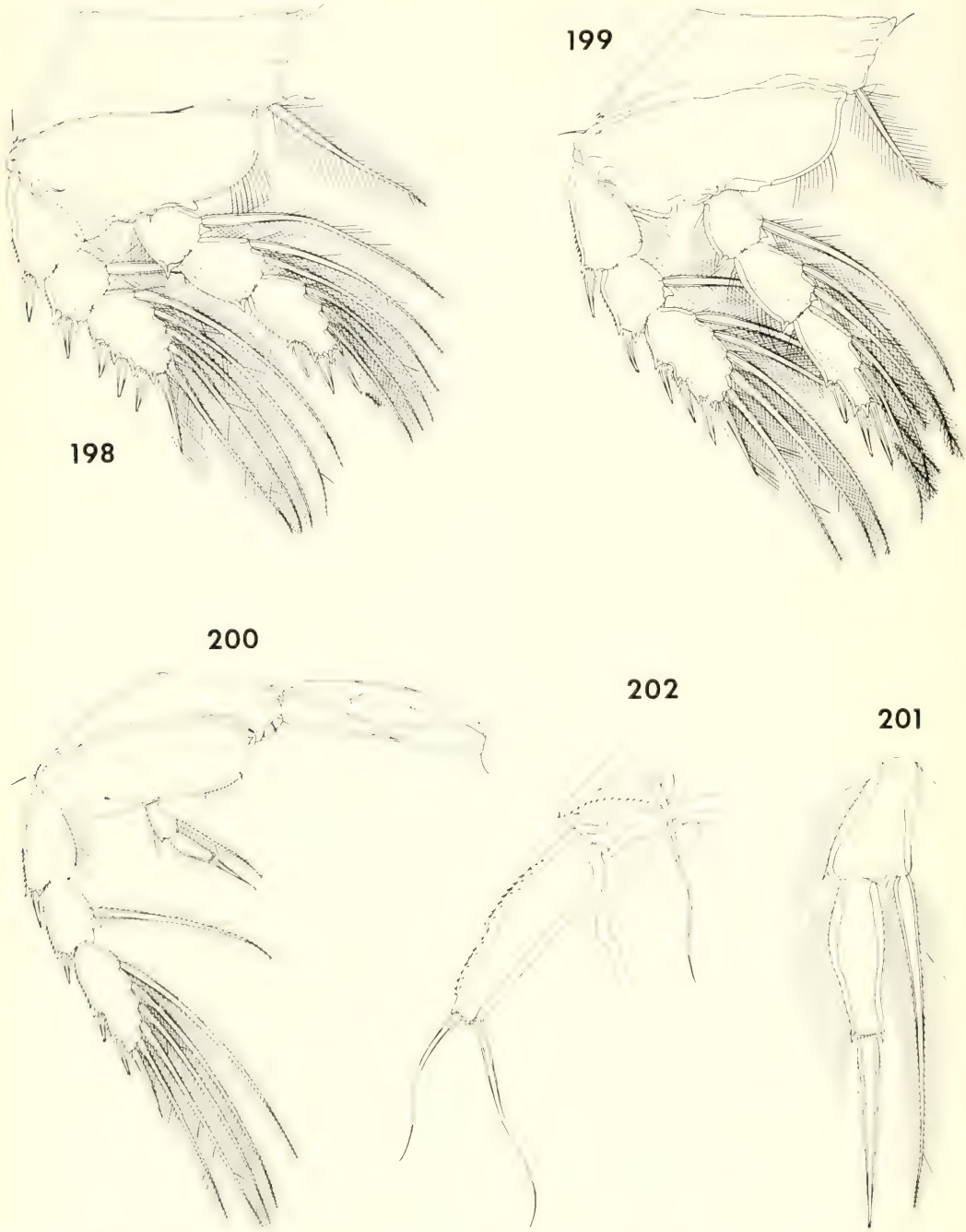
Figures 172–182. *Lichomolgus crassus* n. sp., male. 172, body, dorsal (A); 173, urosome, dorsal (G); 174, caudal ramus, dorsal (E); 175, first antenna, ventral (E); 176, maxilliped, inner (E); 177, leg 1, anterior (E); 178, last segment of endopod of leg 2, anterior (D); 179, last segment of endopod of leg 3, anterior (D); 180, endopod of leg 4, anterior (D); 181, leg 5, dorsal (F); 182, segment of leg 5 and genital segment, ventral (H).



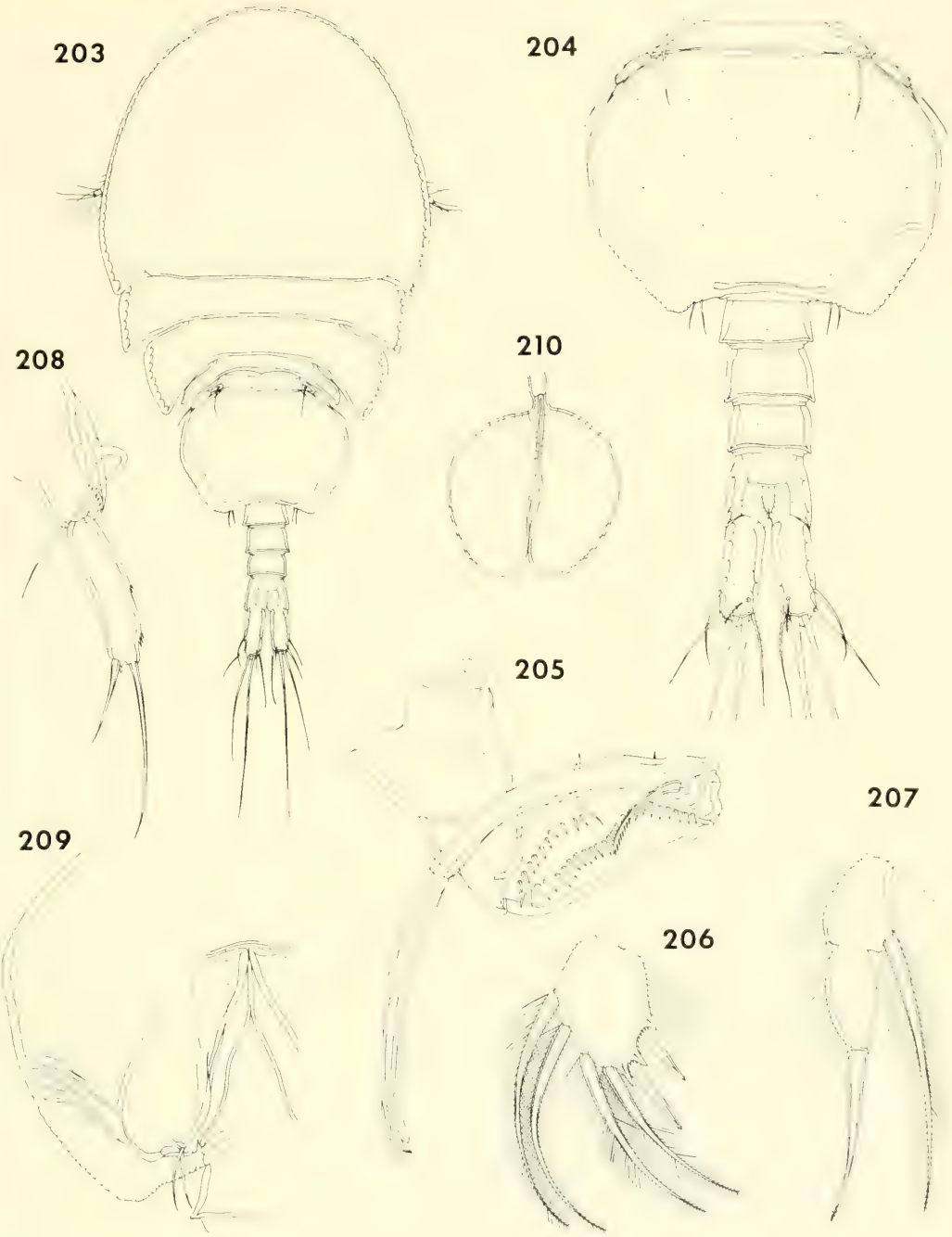
Figures 183–188. *Prionomolgus lanceolatus* n. gen., n. sp., female. 183, body, dorsal (A); 184, urosome, dorsal (B); 185, area of attachment of egg sac, dorsal (F); 186, caudal ramus, dorsal (D); 187, egg sac, ventral (B); 188, cephalosome, ventral (B).



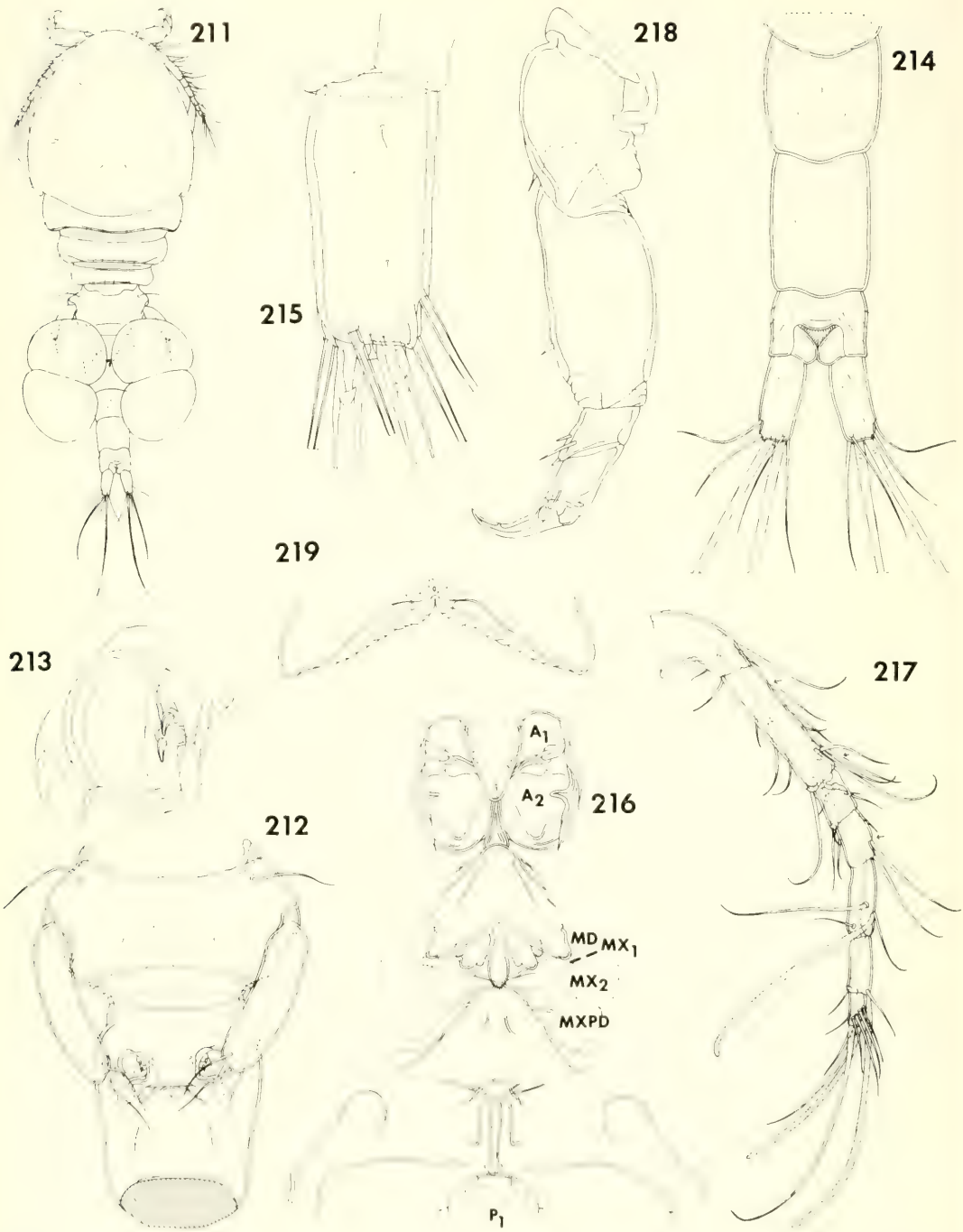
Figures 189–197. *Prionomolgus lanceolatus* n. gen., n. sp., female (continued). 189, first antenna, dorsal (E); 190, second antenna, posterior (E); 191, labrum, ventral (D); 192, mandible, posterior (F); 193, paragnath, posterior (I); 194, first maxilla, posterior (F); 195, second maxilla, anterior (D); 196, maxilliped, outer (F); 197, leg 1 and intercoxal plate, anterior (E).



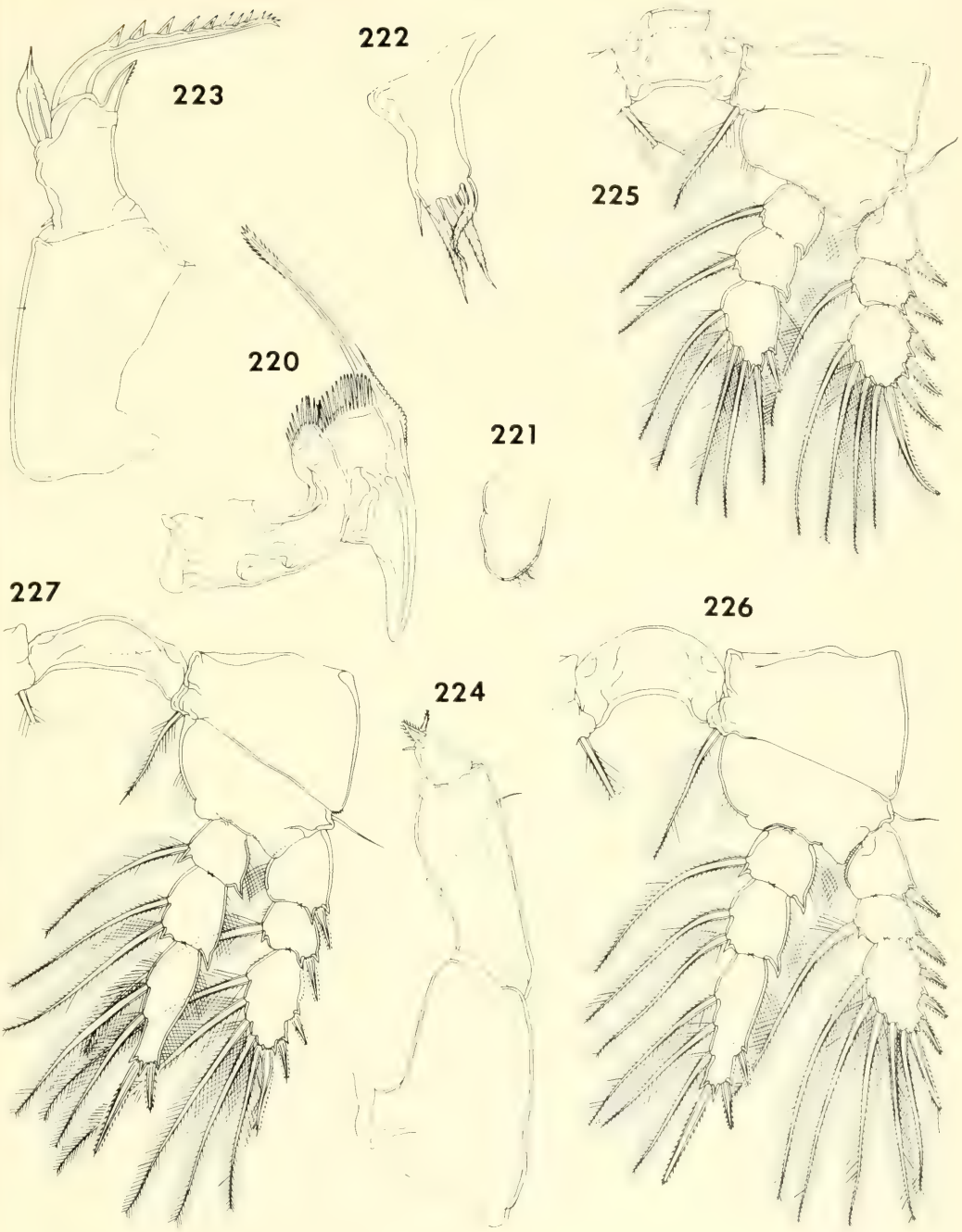
Figures 198–202. *Prionomolgus lanceolatus* n. gen., n. sp., female (continued). 198, leg 2, anterior (E); 199, leg 3, anterior (E); 200, leg 4 and intercoxal plate, anterior (E); 201, endopod of leg 4, anterior (C); 202, leg 5, dorsal (D).



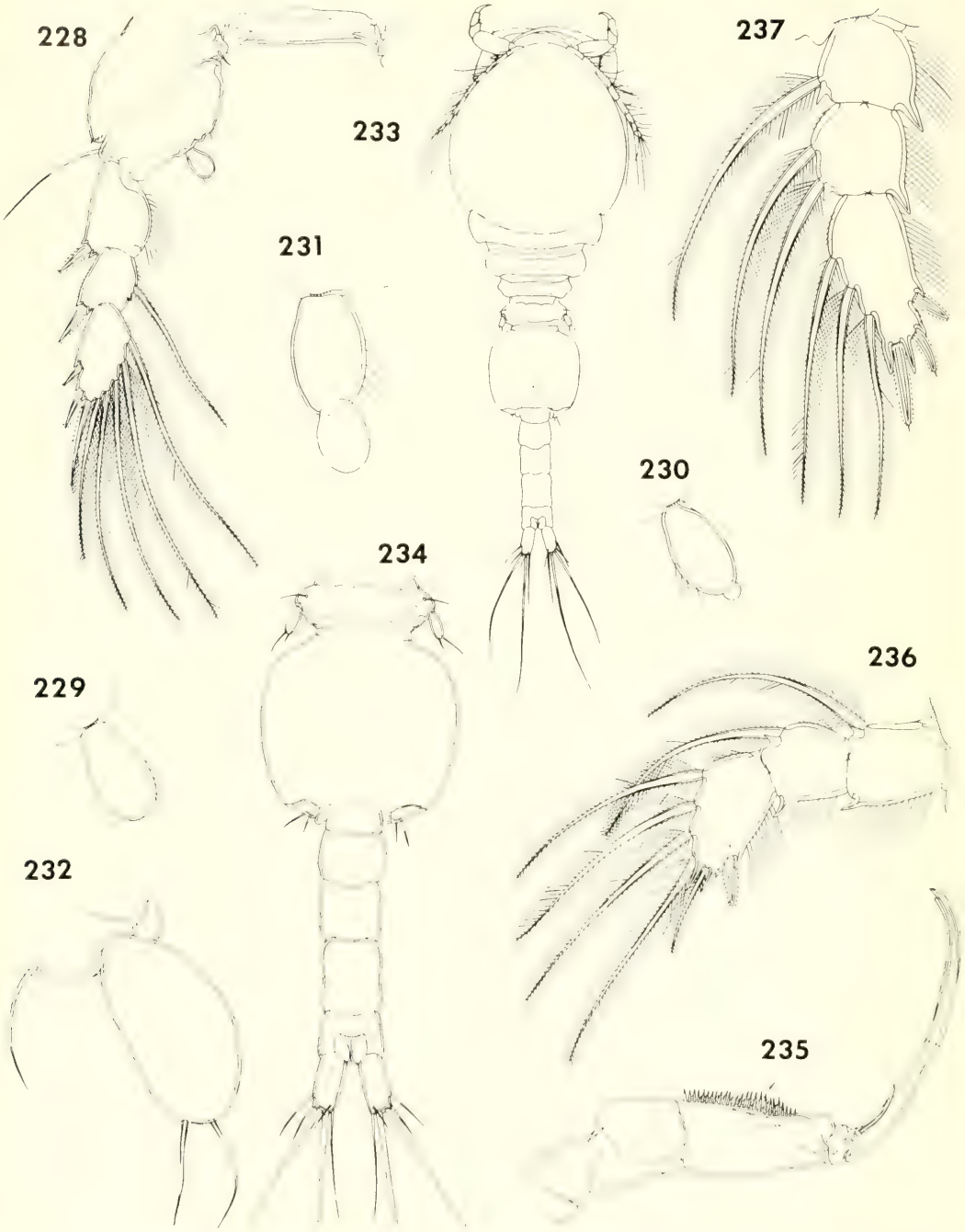
Figures 203–210. *Prionomolgus lanceolatus* n. gen., n. sp., male. 203, body, dorsal (G); 204, urosome, dorsal (H); 205, maxilliped, anterointernal (D); 206, last segment of endopod of leg 1, anterior (F); 207, endopod of leg 4, anterior (C); 208, leg 5, dorsal (F); 209, leg 6, ventral (E); 210, spermatophores, attached to female, lateral (B).



Figures 211–219. *Haplomolgus montiporae* n. gen., n. sp., female. 211, body, dorsal (G); 212, segment of leg 5 and genital segment, dorsal (E); 213, area of attachment of egg sac, dorsal (I); 214, postgenital segments and caudal rami, dorsal (E); 215, caudal ramus, dorsal (C); 216, rostral, oral, and postoral areas, ventral (E); 217, first antenna, with arrows indicating positions of aesthetes in male, posteroventral (D); 218, second antenna, inner (F); 219, edge of labrum, ventral (F).

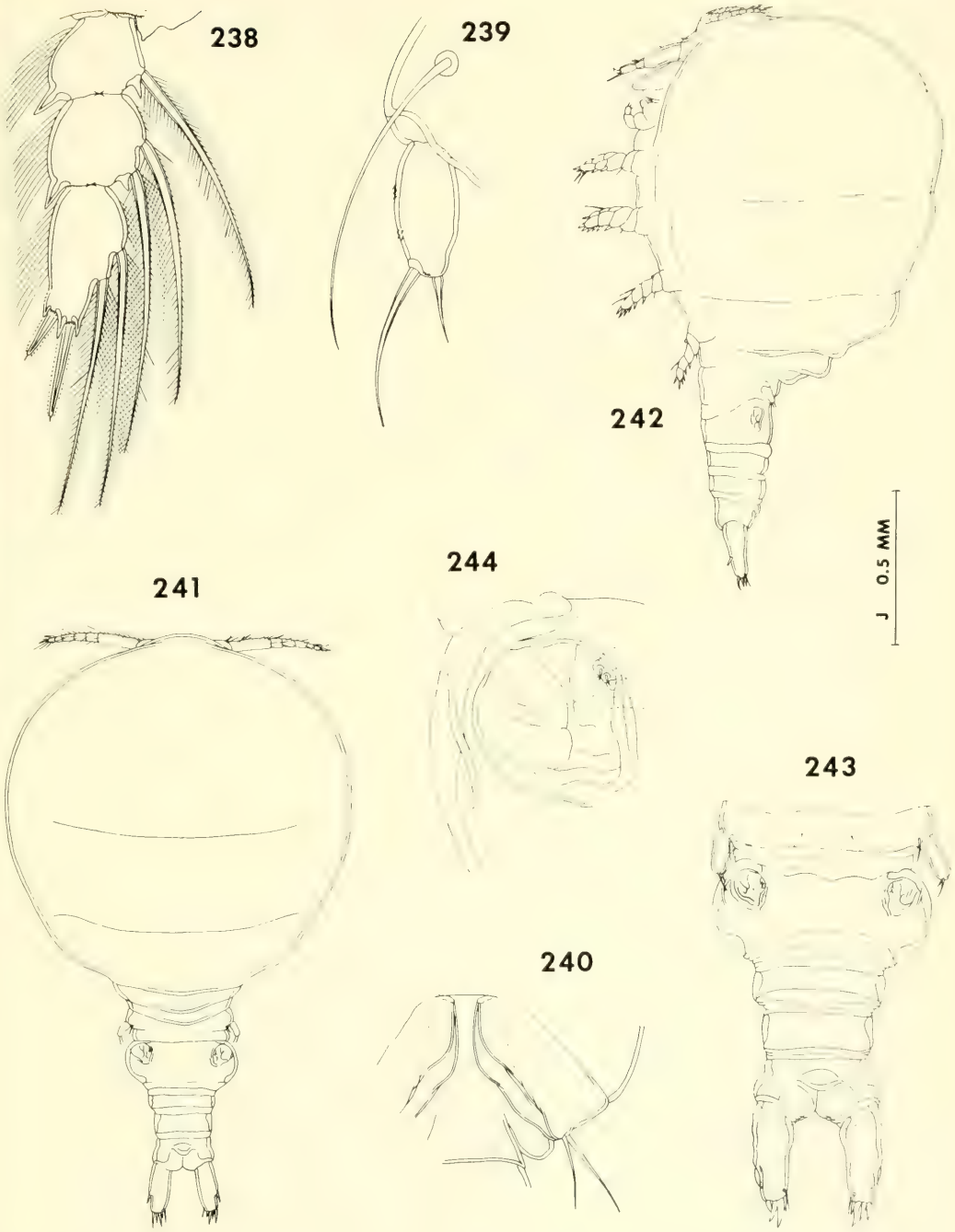


Figures 220–227. *Haplomolgus montiporae* n. gen., n. sp., female (continued). 220, mandible, posterior (C); 221, paragnath, posterior (C); 222, first maxilla, posterior (C); 223, second maxilla, posterior (C); 224, maxilliped, anterior (C); 225, leg 1 and intercoxal plate, anterior (D); 226, leg 2 and intercoxal plate, anterior (D); 227, leg 3 and intercoxal plate, anterior (D).



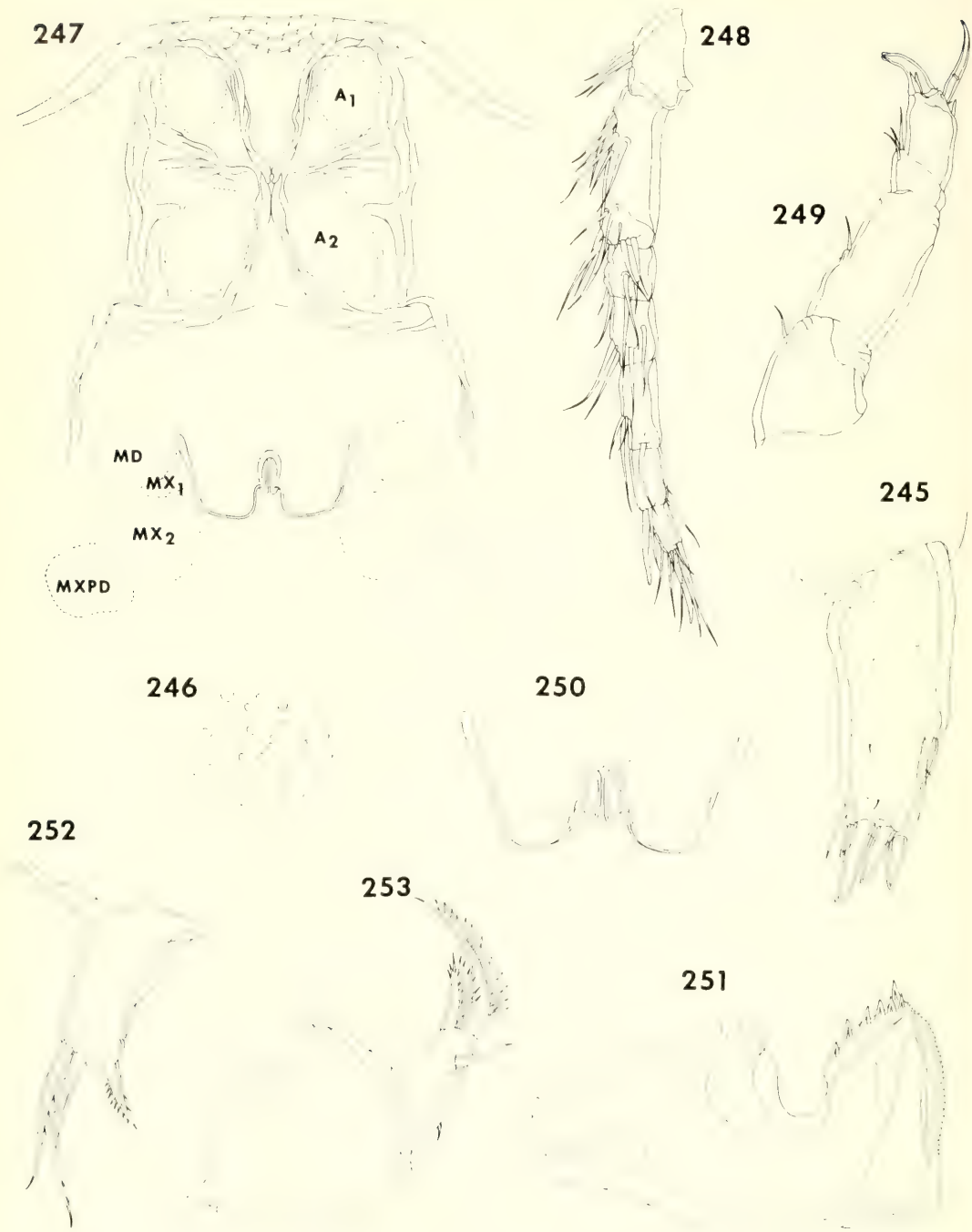
Figures 228–232. *Haplomolgus montiporae* n. gen., n. sp., female (continued). 228, leg 4 and intercoxal plate, anterior (D); 229, endopod of leg 4, anterior (C); 230, endopod of leg 4, anterior (C); 231, endopod of leg 4, anterior (C); 232, leg 5, lateroventral (D).

Figures 233–237. *Haplomolgus montiporae* n. gen., n. sp., male. 233, body, dorsal (G); 234, urosome, dorsal (H); 235, maxilliped, inner (E); 236, endopod of leg 1, anterior (F); 237, endopod of leg 2, anterior (F).

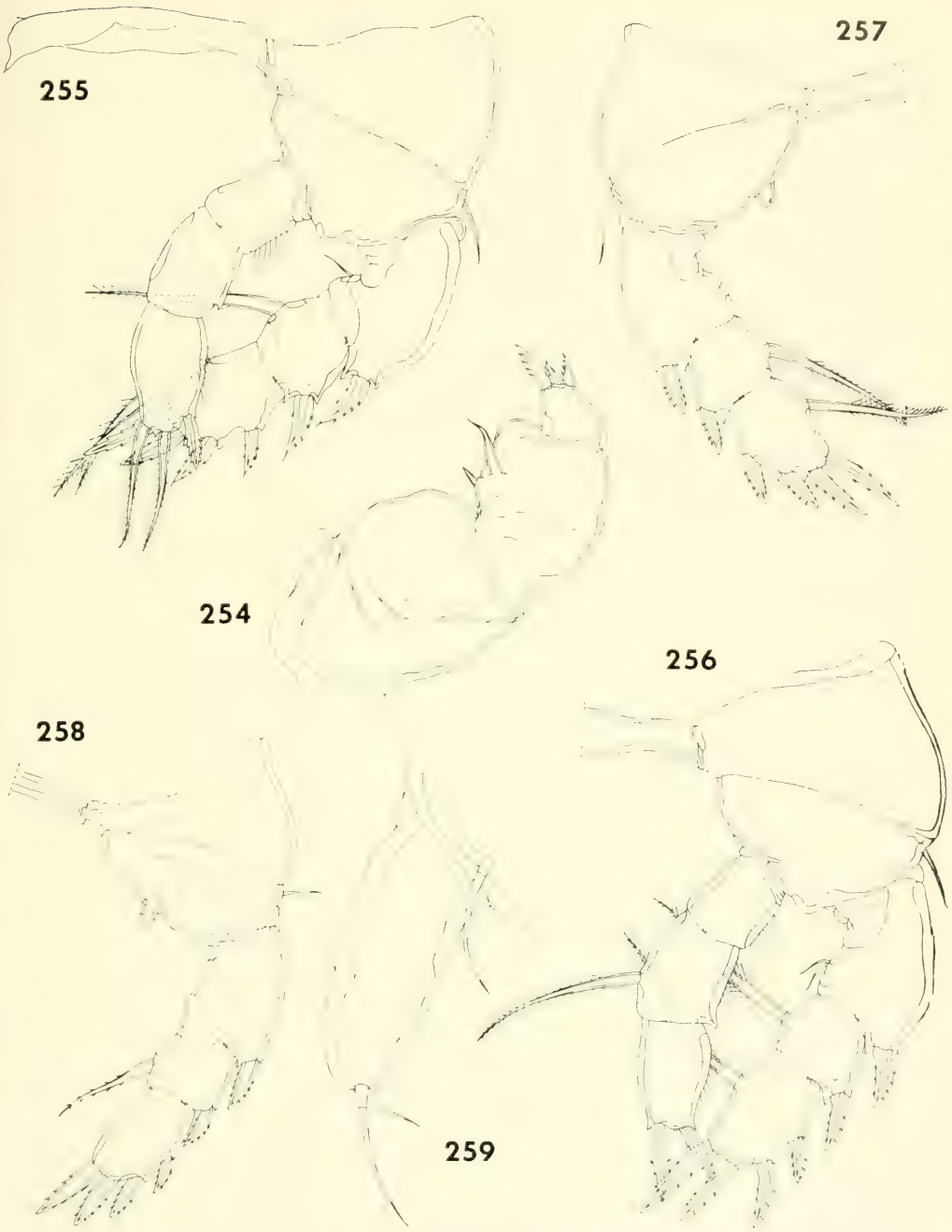


Figures 238–240. *Haplomolgus montiporae* n. gen., n. sp., male (continued). 238, endopod of leg 3, anterior (F); 239, leg 5, dorsal (C); 240, leg 6, ventral (D).

Figures 241–244. *Ravahina tumida* n. gen., n. sp., female. 241, body, dorsal (J); 242, body, lateral (J); 243, urosome, dorsal (G); 244, area of attachment of egg sac, dorsal (D).



Figures 245–253. *Ravahina tumida* n. gen., n. sp., female (continued). 245, caudal ramus, dorsal (E); 246, portion of dorsal surface of segment of leg 1 showing irregular surface of cuticula, dorsal (F); 247, rostral and oral areas, ventral (H); 248, first antenna, anterodorsal (H); 249, second antenna, anterior (H); 250, labrum, ventral (E); 251, mandible, posterior (F); 252, first maxilla, posterior (F); 253, second maxilla, anterior (D).



Figures 254–259. *Ravahina tumida* n. gen., n. sp., female (continued). 254, maxilliped, anterior (D); 255, leg 1 and intercoxal plate, anterior (E); 256, leg 2, anterior (E); 257, leg 3, anterior (E); 258, leg 4, anterior (E); 259, leg 5, dorsal (F).

Bulletin OF THE
Museum of
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Zoology

Xarifiid Copepods (Cyclopoida) Parasitic in Corals in Madagascar

ARTHUR G. HUMES AND JU-SHEY HO

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 11
APRIL 15, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

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Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
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XARIFIID COPEPODS (CYCLOPOIDA) PARASITIC IN CORALS IN MADAGASCAR

ARTHUR G. HUMES[1,2] AND JU-SHEY HO[1]

INTRODUCTION

The family Xarifiidae at present contains only the genus *Xarifia* Humes, 1960. (The genus *Kombia* Humes, 1962, assigned tentatively to this family, belongs more probably to the Lichomolgidae, as pointed out by Humes and Ho, 1968.) Two species, *X. maldivensis* and *X. fimbriata*, were described by Humes (1960) from corals in the Maldive Islands. Nine species are known from corals in the region of Nosy Bé, Madagascar. These are *X. gerlachi*, *X. longipes*, *X. dispar*, *X. reducta*, *X. serrata*, *X. tenuis*, *X. infrequens*, and *X. comata*, all described by Humes (1962), and *X. diminuta* Humes and Ho (1967). This paper deals with nine new species of *Xarifia* and two new species belonging to a new xarifiid genus, collected from corals in the vicinity of Nosy Bé during 1960 and 1963–64.

All collections were made by A. G. Humes, those in 1960 during an expedition of the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition. Type material has been deposited in the United States National Museum. Specimens of several of the new species have been placed in the Museum of Comparative Zoology.

[1] Boston University, Boston, Massachusetts.

[2] Associate in Marine Invertebrates, Museum of Comparative Zoology.

The study of the specimens has been aided by grants (GB-1809 and GB-5838) from the National Science Foundation of the United States.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

The measurement of the length of the body has been made in all cases from specimens in lactic acid and does not include the setae on the caudal rami. In the spine and setal formulas of legs 1–4 the Roman numerals indicate spines and the Arabic numerals represent setae.

The abbreviations used are: A_1 = first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, P_1 = leg 1.

We thank Dr. Donald F. Squires of the United States National Museum for the identifications of corals collected in 1960, and Dr. Michel Pichon, then at the Centre O.R.S.T.O.M. de Nosy Bé, for the determinations of those collected in 1963–64.

The new copepods described in this paper comprise the following:

1) *Xarifia lamellispinosa* n. sp.
   from *Pachyseris speciosa* (Dana)
2) *Xarifia exigua* n. sp.
   from *Pachyseris speciosa* (Dana)
3) *Xarifia decorata* n. sp.
   from *Stylophora pistillata* (Esper)
   and *Stylophora mordax* (Dana)

4) *Xarifia lissa* n. sp.
from *Stylophora pistillata* (Esper) and *Stylophora mordax* (Dana)

5) *Xarifia obesa* n. sp.
from *Pocillopora verrucosa* (Ellis and Solander), *Pocillopora* sp. cf. *P. verrucosa* (E. and S.), and *Pocillopora danae* Verrill

6) *Xarifia brevicauda* n. sp.
from *Alveopora* sp.

7) *Xarifia temnura* n. sp.
from *Montipora sinensis* Bernard

8) *Xarifia anomala* n. sp.
from *Acropora palifera* (Lamarck)

9) *Xarifia hamata* n. sp.
from *Turbinaria* sp.

10) *Orstomella faviae* n. gen., n. sp.
from *Favia* sp.

11) *Orstomella lobophylliae* n. gen., n. sp.
from *Lobophyllia costata* (Dana) and *Lobophyllia corymbosa* (Forskål)

The following represent new host records:

1) *Xarifia dispar* Humes, 1962
from *Echinopora lamellosa* (Esper) and *Echinopora gemmacea* (Lamarck)

2) *Xarifia serrata* Humes, 1962
from *Pocillopora bulbosa* Ehrenberg

KEYS TO THE SPECIES OF THE GENUS *XARIFIA*

Females

1. Endopods of legs 1–4 one-segmented 2
Endopods of legs 1–4 two-segmented 13
2. Region dorsal to fifth legs with two or three processes 3
Region dorsal to fifth legs without processes (or at most a median transverse ridge as in *X. serrata*) 10
3. Region dorsal to fifth legs with two processes 4
Region dorsal to fifth legs with three processes 5
4. Leg 5 with a small free segment (24 × 9 μ); outer element on second segment of exopods of legs 1–4 a seta rather than a spine; body unusually stout, about 4 times longer than wide *obesa*
Leg 5 without a free segment and represented only by three setae; second segment of exopods of legs 1–4 outwardly unarmed; body elongated and slender, 6.7 times longer than wide *fimbriata*
5. Three processes above fifth legs about equal in length 6
Two lateral processes distinctly shorter than median process 9
6. Processes short; caudal ramus small and indistinctly set off from anal segment *gerlachi*
Processes elongated; caudal ramus distinctly set off from anal segment 7
7. Two small lobes between processes; outer element on second segment of exopod of legs 1–4 a seta *maldivensis*
Without knobs between processes; outer element on second segment of exopod of legs 1–4 a spine 8
8. Three processes about equal in length; length of body 0.75 mm *exigua*
Middle process a little shorter than other two; length of body 1.48 mm *longipes*
9. Caudal ramus about 9 times longer than wide; first segment of exopod of legs 1–4 without an outer spine, but instead only a minute spiniform projection *tenuis*
Caudal ramus about 4 times longer than wide; first segment of exopod of legs 1–4 with a distinct (though small) spine *infrequens*
10. Body about 10 times longer than wide; caudal ramus fused with anal segment; postgenital segments fused into a single small segment *temnura*
Body about 6–7 times longer than wide; caudal ramus distinct; postgenital segments not unusually reduced 11
11. Second segment of exopods of legs 1–4 with only a small outer knob; region dorsal to fifth legs not projected *reducta*
Second segment of exopods of legs 1–4 unarmed; region dorsal to fifth legs projected to form a slight transverse ridge 12
12. Leg 5 122 μ long; blade of mandible with small spinules; endopod of leg 2 with two terminal setae *serrata*
Leg 5 72 μ long; blade of mandible with strong teeth; endopod of leg 2 with three terminal setae *lissa*
13. Second segment of exopod of legs 1–4 unarmed *comata*
Second segment of exopod of legs 1–4 with either a spine or a seta 14
14. First and second segments of exopods of legs 1–4 similarly armed with a slender outer spine (almost setiform) *dispar*
These segments not so armed 15

15. First and second segments of exopods of legs 1–4 with a strong outer spine 16
    These segments not so armed (second segment with a small outer spine or a seta) 19
16. Endopod of leg 3 with a terminal seta; length of body 1.90 mm ..... *lamellispinosa*
    Endopod of leg 3 unarmed; length of body 1.27 mm or less 17
17. Endopod of leg 1 unarmed; endopod of leg 2 with three terminal setae ... *anomala*
    Endopods of legs 1 and 2 with two terminal setae 18
18. Endopod of leg 4 with two terminal setae; length of body 0.98 mm ..... *diminuta*
    Endopod of leg 4 unarmed; length of body 1.27 mm ..... *brevicauda*
19. First segment of exopods of legs 1–4 with a strong outer spine; second segment of exopod of leg 1 with a small outer spine, in legs 2–4 with a seta; endopods of legs 1–4 with terminal setae ... *decorata*
    First segment of exopods of legs 1–4 with a strong outer spine; second segment of these exopods with a seta; endopod of leg 2 with a seta and a clawlike spine, endopods of legs 3 and 4 with only a clawlike spine ..... *hamata*

Males

1. Endopods of legs 1–4 one-segmented 2
   Endopods of legs 1–4 two-segmented 13
2. First and second segments of exopod of leg 1 with a distinct outer spine 3
   Both of these segments or only second segment lacking such a spine 6
3. Caudal ramus small and completely or partially fused with anal segment 4
   Caudal ramus more prominent and distinct from anal segment 5
4. Body about 7 times longer than wide; blade of mandible with spinules; second segment of exopods of legs 2–4 with an outer spine ..... *gerlachi*
   Body about 10 times longer than wide; blade of mandible smooth; second segment of exopods of legs 2–4 unarmed ..... *temnura*
5. Terminal setae on endopods of legs 1–4 arranged as 2, 1, 1, 1; length of body, 1.43 mm ..... *longipes*
   Terminal setae on endopods of legs 1–4 arranged as 2, 2, 1, 1; length of body 0.80 mm ..... *exigua*
6. Second segment of exopod of leg 1 with an outer seta 7
   Second segment of exopod of leg 1 unarmed (or at most with only a small outer knob as in *X. reducta*) 8
7. Body unusually stout, about 4 times longer than wide ..... *obesa*
   Body more slender, a little more than 6 times longer than wide ..... *maldivensis*
8. First segment of exopod of leg 1 without a distinct element, having only a minute outer process ..... *tenuis*
   First segment of exopod of leg 1 with a distinct outer element 9
9. First segment of exopod of leg 1 with an outer spine 10
   First segment of exopod of leg 1 with an outer seta ..... *fimbriata*
10. Second segment of exopod of leg 1 with a small outer knob or hyaline seta 11
    Second segment of exopod of leg 1 unarmed 12
11. Second segment of exopod of leg 1 with a small outer knob; concave surface of claw of maxilliped with a row of about twelve long spinules ..... *reducta*
    Second segment of exopod of leg 1 with a small hyaline seta; concave surface of claw of maxilliped serrated ..... *lissa*
12. Concave margin of claw of maxilliped with irregular rounded serrations; body about 8 times longer than wide ..... *serrata*
    Concave margin of claw of maxilliped distally with a few minute teeth; body about 11 times longer than wide ..... *infrequens*
13. Second segment of exopods of legs 1–4 unarmed ..... *comata*
    Second segment of exopods of legs 1–4 with a spine or seta 14
14. Second segment of exopods of legs 1–4 with an outer seta; second segment of endopod of leg 2 with a seta and a clawlike spine ..... *hamata*
    Second segment of exopod of leg 1 with an outer spine; without a clawlike spine on second segment of endopod of leg 2 15
15. Second segment of exopods of legs 2–4 with an outer seta ..... *decorata*
    Second segment of exopods of legs 2–4 with an outer spine 16
16. Spines on first two segments of exopods of legs 1–4 slender, almost setiform ..... *dispar*
    Spines on these segments clearly spiniform rather than setiform 17
17. With a terminal seta on endopod of leg 3, formula for terminal elements on endopods of legs 1–4 being 2, 2, 1, 1 ..... *lamellispinosa*
    Without a terminal seta on endopod of leg 3 18
18. Without terminal setae on endopod of leg 1, formula for terminal elements of endopods of legs 1–4 being 0, 3, 0, 0 ..... *anomala*

With two terminal setae on endopod of leg 1 19

19. Without terminal setae on endopod of leg 4, formula for terminal elements on endopods of legs 1–4 being 2, 2, 0, 0; postgenital region shortened with segments fused; concave margin of claw of maxilliped with a serrated excrescence ..... *brevicauda*

With two terminal setae on endopod of leg 4, formula for terminal elements on endopods of legs 1–4 being 2, 2, 0, 2; postgenital region not shortened; concave margin of claw of maxilliped without a serrated excrescence ..... *diminuta*

SYSTEMATIC DESCRIPTION

XARIFIIDAE Humes, 1960

XARIFIA Humes, 1960

Xarifia lamellispinosa n. sp.

Figs. 1–22

Type material.—13 females and 14 males from a colony of *Pachyseris speciosa* (Dana) in a depth of 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, Madagascar. Collected June 12, 1964. Holotype female, allotype, and 21 paratypes (10 females and 11 males) deposited in the United States National Museum, Washington; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Pachyseris speciosa*).—3 females and 11 males in 3 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, September 3, 1963; 1 male in 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, October 18, 1963.

Female.—Body (Figs. 1 and 2) slender, about 7 times longer than wide. Length 1.90 mm (1.84–2.00 mm) and greatest width 0.27 mm (0.26–0.27 mm), based on 10 specimens. Segmentation not well defined externally. Region dorsal to fifth legs bearing three long posteriorly directed processes, the median one slightly shorter than the lateral ones. Genital and postgenital segments together a little less than one-fourth of total body length. Areas of attachment of egg sacs located dorsally (Fig. 3). Caudal ramus (Fig. 4) about 51 × 28 μ in greatest dimensions, a little less than 2 times longer than wide; with four short naked setae (one outer and subterminal, the others terminal) and surficial hairs. Egg sac (Fig. 3) 340 μ in length, containing five eggs (except in one female where the sac on one side had only four), each egg about 109 μ in average diameter.

Rostral area a rounded lobe between bases of first antennae and covered with short hairs (Fig. 5). First antenna (Fig. 6) short (about 60 μ in length without setae) and apparently 3-segmented. With numerous naked setae, the armature being 3, 22 + 1 aesthete, and 9 + 2 aesthetes. Second antenna (Fig. 7) 4-segmented, the formula being 1, 1, 2, and I, 1. Recurved claw and seta on last segment both 17 μ long.

Labrum (Fig. 8) with trilobate free margin, the middle lobe slightly indented. Mandible (Fig. 9) with blade having four teeth and a recurved tip. Paragnath absent. First maxilla (Fig. 10) a small lobe with two naked setae. Second maxilla (Fig. 11) probably 2-segmented, second segment bearing two unequal inner setae and a distal lamellate expansion with a terminal knob. Maxilliped (Fig. 12) apparently 3-segmented, first segment with an outer lobate expansion, second segment bearing two inner setae and a lobate expansion, third segment with two small spiniform elements and terminating in a short claw. Relationships of head appendages as in Figure 13.

Legs 2–4 with general form and segmentation like that of leg 1 (Fig. 14), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_2	protopod 0–0; 1–0	exp 1–0; 1–0; I, 3	end 0–0; 2
P_3	protopod 0–0; 1–0	exp 1–0; 1–0; I, 2	end 0–0; 2
P_4 and P_5	protopod 0–0; 1–0	exp 1–0; 1–0; I, 2	end 0–0; 1

In all four legs posterior surface of protopod with a patch of hairs and basis with an outer naked seta. Exopods with stout spines recurved posteriorly and bearing

conspicuous lamellae (Figs. 14, 15, and 16); three slender setae at inner base of terminal spine in leg 1, two such setae in legs 2, 3, and 4. Endopods with few hairs on outer margins of both segments, and with two terminal setae in legs 1 and 2 but only one such seta in legs 3 and 4. Leg 4 (not drawn) armed as in leg 3. Intercoxal plate V-shaped in leg 1, less so in succeeding legs.

Leg 5 (Fig. 17) elongated and slender, with its free segment not clearly delimited from body. Segment about 110 μ in length and tapered distally, with two unequal terminal naked setae 11 and 37 μ long. A slender seta arising from body wall dorsal to base of segment. Leg 6 absent.

Color in life in transmitted light slightly brownish, eye red.

Male.—Body (Figs. 18 and 19) slender, almost as long as female. Length 1.83 mm (1.76–1.87 mm) and greatest width 0.22 mm (0.19–0.24 mm), based on 10 specimens. Without external segmentation. Caudal ramus about 34×25 μ, weakly set off from anal segment (Fig. 20).

Rostral area as in female. First antenna like that of female, but with four aesthetes, one being added on midanterior margin of middle segment. Second antenna, labrum, mandible, first maxilla, and second maxilla resembling those in female. Paragnath absent. Maxilliped (Fig. 21) 4-segmented. First segment short and unarmed. Second large and swollen with two inner setae. Third very short and unarmed. Fourth segment forming a terminal claw 57 μ along its axis, with a prominent conical process on its inner concave margin and trifurcated at its tip, bearing two proximal unequal setae (one sclerotized basally but hyaline and obtuse distally, the other hyaline throughout).

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 22) having its small free segment (12×8 μ) not distinctly delimited from body and bearing two unequal terminal naked setae 14 and 31 μ long. Leg 6 (Fig. 20) represented by a posteroventral flap on genital segment bearing two small setae.

Spermatophore not observed.

Color as in female.

Etymology.—The specific name *lamellispinosa* is a combination of the Latin words *lamella* = a lamella, and *spinosus* = having spines, in allusion to the conspicuous lamellae on the spines of the exopods of legs 1–4.

Comparison with related species.—Only three of the eleven known species in the genus *Xarifia* resemble the new species in having three long processes dorsal to the fifth legs in the female, in having an elongated leg 5 in the female, and in having 2-segmented endopods in legs 1–4. These are *X. dispar* Humes, 1962, *X. comata* Humes, 1962, and *X. diminuta* Humes and Ho, 1967. From each of these *X. lamellispinosa* may be readily distinguished. *X. dispar* has a slender, almost straight spine instead of a stout recurved spine on the first and second segments of the exopods of legs 1–4. *X. comata* lacks a spine on the second segment of these legs, and has two terminal setae on the endopod of leg 3. *X. diminuta* lacks setae on this endopod, and the mandible has a smooth blade without teeth. Furthermore, *X. lamellispinosa* is considerably larger than these three species, with its size range not overlapping any of them.

Xarifia exigua n. sp.

Figs. 23–43

Type material.—21 females and 28 males from a colony of *Pachyseris speciosa* (Dana) in a depth of 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, Madagascar. Collected October 18, 1963. (One male of *X. lamellispinosa* also was washed from this colony.) Holotype female, allotype, and 39 paratypes (16 females and 23 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 23 and 24) slender, about 7.5 times longer than wide.

Length 0.75 mm (0.71–0.80 mm) and greatest width 0.10 mm (0.10–0.11 mm), based on 10 specimens. External segmentation not well defined. Region dorsal to fifth legs bearing three long posteriorly directed processes of about equal length. Genital and postgenital segments together about one-fourth of total body length. Areas of attachment of egg sacs situated dorsally (Fig. 25). Caudal ramus (Fig. 26) 41 × 11 μ, about 4 times longer than wide, with the usual four setae, all relatively long and slender. Egg sac unknown.

Rostral area rounded (Fig. 27). First antenna (Fig. 27) short, about 50 μ in length, and apparently 3-segmented. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 28) 4-segmented, with formula same as in previous species. Slender claw and adjacent seta on last segment both 18 μ long.

Labrum (Fig. 29) with trilobate free margin, slightly indented medially. Mandible (Fig. 30) with smooth pointed blade. Paragnath absent. First maxilla (Fig. 31) the usual small lobe with two naked setae. Second maxilla (Fig. 32) 2-segmented, resembling that of *X. diminuta*, second segment having two unequal inner setae and a terminal lamellate process. Maxilliped (Fig. 33) probably 3-segmented, but segmentation obscure. Region of second segment with two inner setae and a lobate expansion; that of third segment with two minute elements and lacking a claw. Relationships of head appendages as in Figure 34.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 35), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod 0–0; 1–0	exp end	I–0; I–0; I, 2 2
P_3 and P_4	protopod 0–0; 1–0	exp end	I–0; I–0; I, 2 1

In all four legs, basis with an outer naked seta. Exopod spines rather long and slender, not strongly recurved. Small spiniform process near base of spine on first exopod segment. Endopods consisting of a single segment provided on outer margin with a proximal setule followed by a row of hairs. Endopods of legs 1 and 2 with two terminal setae, those of legs 3 (Fig. 36) and 4 with a single such seta. Intercoxal plate of leg 1 rather wide (Fig. 35), those of succeeding legs narrower.

Leg 5 (Fig. 37) elongated and slender, with free segment weakly delimited from body. Segment about 100 μ long and tapered distally, the two terminal setae 13 and 24 μ in length. Leg 6 absent.

Color in life in transmitted light pale brownish, eye red.

Male.—Body (Figs. 38 and 39) slender, about as long as female. Length 0.80 mm (0.76–0.85 mm) and greatest width 0.10 mm (0.10–0.10 mm), based on 10 specimens. Without external segmentation. Caudal ramus (Fig. 40) smaller than in female, 19 × 10 μ.

Rostral area as in female. First antenna resembling that of female, but with an additional aesthete on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla like those in female. Paragnath absent. Maxilliped (Fig. 41) segmented and armed as in previous species. Second segment with two inner setae. Fourth segment forming a claw 31 μ along its axis, with a conical process on its inner concave margin and bifurcated at its tip (in one male trifurcated on one maxilliped), bearing the usual two unequal proximal setae.

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 42) with a small segment not well delimited from body and bearing two unequal setae. Leg 6 (Fig. 43) the usual posteroventral flap on genital segment with two setae.

Spermatophore not observed.

Color as in female.

Etymology.—The specific name *exigua*, from Latin = small in size, refers to the small size of this species, the smallest of any species of *Xarifia* thus far described.

Comparison with related species.—There are eight known species of *Xarifia* in which the endopods of legs 1–4 are 1-segmented, thus resembling *X. exigua*. These are *X. maldivensis* Humes, 1960, *X. fimbriata* Humes, 1960, *X. gerlachi* Humes, 1962, *X. longipes* Humes, 1962, *X. reducta* Humes, 1962, *X. serrata* Humes, 1962, *X. tenuis* Humes, 1962, and *X. infrequens* Humes, 1962. In only two of these, *X. gerlachi* and and *X. longipes*, does the second exopod segment of legs 1–4 bear a spine, as in the new species; in the others there may be a seta, a small knob, or no element at all. *X. exigua* may be readily distinguished from *X. gerlachi* which has three short processes above the fifth legs in the female and a larger size (female 2.04 mm, male 0.89 mm), and from *X. longipes* which has three very long processes (the middle one slightly shorter than the others) dorsal to the fifth legs in the female, relatively very long caudal rami, and a larger size (female 1.48 mm, male 1.43 mm).

Xarifia decorata n. sp.

Figs. 44–69

Type material.—30 females and 22 males from several colonies of *Stylophora pistillata* (Esper) in a depth of 0.5 m, Navetsy, Nosy Bé, Madagascar. Collected September 24, 1964. Holotype female, allotype, and 38 paratypes (22 females and 16 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 19 females and 14 males in 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, August 4, 1963; 14 females and 12 males in 3 m, Ambariobe, August 13, 1963; 5 females and 10 males in 0.5 m, Ambariobe, October 6, 1963; and 1 male in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964. From *Stylophora mordax* (Dana): 4 females in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963.

Female.—Body (Figs. 44 and 45) slender, about 6.8 times longer than wide. Length 1.49 mm (1.45–1.53 mm) and greatest width 0.22 mm (0.21–0.22 mm), based on 10 specimens. External segmentation poorly defined. Region dorsal to fifth legs bearing three long slender posteriorly directed processes (Fig. 46) of about equal length (220 μ). (In one female carrying a spermatophore these processes were shorter, about 165 μ, and not as slender.) Genital and postgenital segments together a little less than one-fourth of total body length. Areas of attachment of egg sacs located dorsally. Caudal ramus (Fig. 47) elongated, 88 × 19 μ, about 4.6 times longer than wide, and arched dorsally as in Figure 46; bearing one outer subterminal seta and four terminal setae, all relatively short and naked. Egg sac (Fig. 45) containing 2, 3, or 4 eggs in a row, each egg about 122 × 166 μ. Surface of body covered with fine setules as in Figure 46.

Rostral area (Fig. 48) forming a tongue-shaped lobe bearing setules between bases of antennae and projecting a little beyond anterior margin of head in dorsal view (Fig. 49). First antenna (Fig. 50) short, about 54 μ, and apparently 3-segmented, though second and third segments show partial division. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 51) 4-segmented and armed as in two previous species. Terminal claw very slender, 13 μ long, and seta adjacent to it 18 μ.

Labrum (Fig. 52) not trilobed, but indented medially. Mandible (Fig. 53) with smooth pointed blade. Paragnath absent. First maxilla (Fig. 54) the usual small lobe with two naked setae. Second maxilla (Fig. 55) 2-segmented, second segment bearing two unequal hyaline setae and projected terminally to form a broad lamellate lobe with hyaline margins. Maxilliped (Fig. 56) with obscure segmentation, region of second segment bearing two small inner setae and two lobate expansions, that of third segment forming two spinelike processes.

Relationships of head appendages as in Figure 57.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 58), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1	protopod 0–0;	1–0 exp	I–0; I–0; I, 3
		end	0–0; 3
P_2	protopod 0–0;	1–0 exp	I–0; 1–0; I, 2
		end	0–0; 3
P_3 and P_4	protopod 0–0;	1–0 exp	I–0; 1–0; I, 2
		end	0–0; 1

In all four legs, basis with an outer naked seta and inner group of long setules. Second segment of exopod of leg 1 with a small outer spine; in legs 2 (Fig. 59), 3, and 4 this spine replaced by a small hyaline seta. Inner margins of exopod segments with long hairlike setules. Endopods of all four legs with similar setules on both margins of first segment and on outer margin of second segment. Legs 1 (Fig. 58) and 2 with three terminal setae on endopod; legs 3 (Fig. 60) and 4 with a single such seta. Intercoxal plate of leg 1 narrow and U-shaped (Fig. 58), those of succeeding legs much narrower and V-shaped.

Leg 5 (Fig. 61) elongated and tapered distally, the free segment about 150 μ long and fused with body, the two terminal setae 35 and 37 μ in length. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red.

Male.—Body (Figs. 62 and 63) slender, a little shorter than female. Length 1.27 mm (1.25–1.28 mm) and greatest width 0.17 mm (0.16–0.17 mm), based on 10 specimens. Only slight indication of external segmentation. Caudal ramus (Fig. 64) much shorter than that of female, 24 × 14 μ. Body surface with fewer and less conspicuous setules than in female.

Rostral area like that of female. First antenna similar to that of female, but with an additional aesthete on second segment. Second antenna as in female. Labrum (Fig. 65) resembling that of female, but with outer corners projected. Mandible, first maxilla, and second maxilla like those of female. Paragnath absent. Maxilliped (Fig. 66) segmented and armed as in two previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw and bearing two unequal setae. Claw 67 μ along its axis, showing a line of partial division about midway; its inner concave margin with a row of dentiform spinules and its tip bifurcated.

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 67) reduced to a slight ridge bearing two setae 22 and 24 μ in length, with a third seta arising from the body nearby. Leg 6 (Fig. 68) the usual posteroventral flap on genital segment with two setae.

Spermatophore (Fig. 69), attached to female, elongated, 277 × 55 μ, not including the short neck.

Color as in female.

Etymology.—The specific name *decorata*, from Latin = decorated, alludes to the many setules on the body surface and on legs 1–4.

Comparison with related species.—Like *X. dispar* Humes, 1962, *X. comata* Humes, 1962, *X. diminuta* Humes and Ho, 1967, and *X. lamellispinosa*, *X. decorata* has 2-segmented endopods in legs 1–4. The new species may, however, be readily distinguished from each of these four species by the nature of the outer elements on the first and second segments of the exopods of legs 1–4. These segments in *X. dispar* bear a slender spine. In *X. comata* the first segment has a minute spine and the second is unarmed. In *X. diminuta* and *X. lamellispinosa* both segments bear a well developed stout spine. Furthermore, in none of the four species does the claw of the male maxilliped have an inner row of dentiform spinules, as in the new species.

Xarifia lissa n. sp.
Figs. 70–90

Type material.—9 females and 12 males from *Stylophora pistillata* (Esper) in depth of 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected August 4, 1963. (Nine-

teen females and 14 males of *X. decorata* were also recovered from this colony.) Holotype female, allotype, and 15 paratypes (6 females and 9 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 2 females and 1 male in 3 m, Ambariobe, August 13, 1963; 7 females and 6 males in 0.5 m, Ambariobe, October 6, 1963. From *Stylophora mordax* (Dana): 2 females and 1 male in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963.

Female.—Body (Figs. 70 and 71) moderately slender, about 6 times longer than wide. Length 1.40 mm (1.36–1.50 mm) and greatest width 0.23 mm (0.20–0.25 mm), based on 7 specimens. External segmentation weakly defined. Region dorsal to fifth legs smooth, without processes, in lateral view (Fig. 72) raised dorsally. Genital and postgenital segments together about one-fifth of total body length. Areas of attachment of egg sacs located dorsolaterally (Fig. 72). Caudal ramus (Fig. 73) moderately elongated, 41 × 19 μ (width taken at middle), about twice as long as wide; armed with a subterminal outer seta and four terminal setae, one of them very short. Egg sac (Fig. 71) containing 2 or 3 eggs in a row, eggs somewhat variable in size, distalmost egg in figure 174 × 104 μ. Surface of body with scattered short hairs.

Rostral area as in *X. decorata*. First antenna (Fig. 74) 3-segmented and short, about 45 μ in length. Armature: 3, 18 + 1 aesthete, and 6 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 75) 4-segmented and armed as in three previous species. Terminal claw relatively short, 8 μ, and adjacent seta long, 25 μ.

Labrum (Fig. 76) trilobed, the middle lobe much expanded and not indented medially. Mandible (Fig. 77) with its blade having three relatively large inner teeth, two smaller outer teeth, and a recurved tip. Paragnath absent. First maxilla (Fig. 78) a small lobe with two setae. Second maxilla (Fig. 79) 2-segmented, second segment bearing two unequal elements but lacking a lamellate process. Maxilliped (Fig. 80) probably 3-segmented, but segmentation obscure. Region of second segment bearing two small setae, that of third segment unarmed except for a conical terminal process. Relationships of head appendages as in Figure 81.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 82), exopods 3-segmented, endopods 1-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod	0–0; 1–0	exp	I–0; 0–0; I, 2
			end	3
P_3 and P_4	protopod	0–0; 1–0	exp	I–0; 0–0; I, 2
			end	1

In all four legs, basis with an outer naked seta and an inner group of small setules. Second segment of exopods unarmed (Fig. 82). Endopods of legs 1 and 2 with three terminal setae, endopod of legs 3 (Fig. 83) and 4 with a single such seta. Intercoxal plates in all four legs very narrow and V-shaped.

Leg 5 (Fig. 84) moderately elongated and tapered distally, the free segment partially fused with body and about 72 μ in length. Two terminal setae offset on end of leg, unequal, 24 and 35 μ long. Seta on body near free segment short. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red.

Male.—Body (Figs. 85 and 86) elongated and slender, only a little shorter than female. Length 1.32 mm (1.24–1.40 mm) and greatest width 0.16 mm (0.15–0.16 mm), based on 10 specimens. External segmentation weakly developed. Caudal ramus similar to that of female but smaller, 34 × 14 μ. Body surface with fewer small hairs than in female.

Rostral area like that of female. First antenna (Fig. 87) resembling that of female, but an aesthete added on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath absent. Maxilliped (Fig.

88) segmented and armed as in three previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw, bearing two unequal setae. Claw 63 μ along its axis, with its inner concave margin serrated and its tip bifurcated.

Legs 1–4 segmented as in female. Armature as in female except for second exopod segment of leg 1 where there is a small outer hyaline seta (Fig. 89). This seta absent on legs 2–4.

Leg 5 reduced to 3 setae as in *X. decorata*, without a free segment. Leg 6 (Fig. 90) the usual posteroventral flap on genital segment with two setae.

Spermatophore (seen only inside male, as in Figure 86) elongated.

Color in life as in female.

Etymology.—The specific name *lissa*, from the Greek word λισσός = smooth or bare, refers to the absence of processes on the region dorsal to the fifth legs in the female.

Comparison with related species.—Only two other described species of *Xarifia* lack processes on the region dorsal to the fifth legs in the female. These are *X. reducta* Humes, 1962, and *X. serrata* Humes, 1962. *X. reducta* is smaller (female 1.06 mm, male 0.91 mm), the second exopod segment of legs 1–4 bears a small knob, and the male maxilliped is slender, with the claw bearing a row of dentiform spinules. *X. serrata* has a relatively longer leg 5 in the female, the blade of the mandible bears several small spinules, the maxilliped of the female bears on the third segment a terminal seta and an elongated blunt process and a minute subterminal process, the claw of the male maxilliped has larger serrations, and the second exopod segment of leg 1 in the male is unarmed. The new species thus appears to be close to *X. serrata*, but differs from it in the several respects mentioned.

Xarifia obesa n. sp.
Figs. 91–113

Type material.—8 females and 10 males from *Pocillopora verrucosa* (Ellis and Solander) in 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected November 2, 1960. (*X. comata* Humes and *X. serrata* Humes were also collected from this colony of coral.) Holotype female, allotype, and 12 paratypes (5 females and 7 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Pocillopora verrucosa*: 1 female, 2 males, and 1 immature specimen in 2 m, Pte. Mahatsinjo, October 26, 1960. From *Pocillopora* sp. cf. *P. verrucosa*: 9 females, 7 males, and 2 immature specimens in 2 m, west of Pte. Mahatsinjo, October 18, 1960. From *Pocillopora danae* Verrill: 3 females, 2 males, and 1 immature specimen in 6 m, Tany Kely, a small island to the south of Nosy Bé, December 28, 1963.

Female.—Body (Figs. 91 and 92) stouter than in other species of *Xarifia*, about 4 times longer than wide. Length 1.34 mm (1.21–1.48 mm) and greatest width 0.34 mm (0.29–0.35 mm), based on 8 specimens. External segmentation indicated by slight swellings. Region dorsal to fifth legs on each side with a posteriorly directed process. Genital and postgenital segments together about one-third of total body length. Areas of attachment of egg sacs located dorsolaterally (Fig. 93). Egg sac (Fig. 94) about 300 × 240 μ, containing seven eggs in a cluster, each egg about 130 μ in diameter. Caudal ramus (Fig. 95) about 70 μ long and fused with body, rather pointed, with its small spherical tip set off from the proximal part. Armed with an outer marginal seta and three terminal setae, all naked. Body surface with a few small hairs.

Rostral area (Fig. 96) somewhat quadrate, with broadly rounded posterior margin. First antenna (Fig. 97) 3-segmented and short, about 40 μ in length. Armature: 3, 17 + 1 aesthete, and 4 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 98) 3-segmented, the last two seg-

ments being fused. Armature as in previous four species; terminal claw strongly recurved, about 20 μ along its axis, and adjacent seta 16 μ.

Labrum (Fig. 99) with projected corners. Mandible (Fig. 100) with two rows of spinules on blade. Paragnath not seen. First maxilla (Fig. 101) a small lobe with two unequal naked setae. Second maxilla (Fig. 102) globose and highly modified, without definite segmentation, the region of second segment indicated by a pair of small setae and a more distal seta and minute process. Maxilliped (Fig. 103) probably 3-segmented, with two small setae on region of second segment, and two processes and a small seta on third segment. Relationships of head appendages as in Figure 104.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 105), exopods 3-segmented, endopods 1-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod 0–0; 1–0	exp	1–0; 1–0; I, 2
		end	3
P_3 and P_4	protopod 0–0; 1–0	exp	1–0; 1–0; I, 2
		end	1

In all four legs, basis with an outer seta. Second segment of exopods with a small hyaline seta instead of a recurved spine, as in Figure 105. Endopods of legs 1 (Fig. 105) and 2 with three terminal setae, endopods of legs 3 (Fig. 106) and 4 with a single such seta. Intercoxal plate of leg 1 wide and not indented, those of succeeding legs narrower.

Leg 5 (Fig. 107) relatively small (cf. Figs. 91 and 93), about 24×9 μ (width taken at middle), with two terminal setae 18 and 22 μ long. Leg 6 absent.

Color in life in transmitted light opaque, intestine greenish with red globules, eye red, egg sacs tinged with red.

Male.—Body (Figs. 108 and 109) stouter than in other species, approximately 4 times longer than wide, and only a little shorter than female. Length 1.21 mm (1.14–1.30 mm) and greatest width 0.29 mm (0.26–0.31 mm), based on 10 specimens. External segmentation weakly developed. Caudal ramus similar to that of female but shorter, 55 μ in length.

Rostral area as in female. First antenna like that of female, but an additional aesthete on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath not seen. Maxilliped (Fig. 110) segmented and armed as in four previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw, bearing two setae, one proximal and the other near middle of concave margin. Distal part of this margin slightly serrated and tip of claw minutely trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 111) reduced to a small lobe with two terminal setae and an adjacent seta arising from body. Leg 6 (Figs. 112 and 113) the usual posteroventral flap on genital segment with two setae.

Spermatophore (seen only inside male, as in Figure 109) elongated.

Color in life as in female.

Etymology.—The specific name *obesa*, from Latin = fat or swollen, alludes to the unusually stout body.

Comparison with related species.—*X. fimbriata* Humes, 1960, is the only other species of *Xarifia* which has in the female two long processes dorsal to the fifth legs. This species may be easily separated from *X. obesa*, however, by its fifth legs which lack a distinct segment. From all species in the genus *X. obesa* may be distinguished by its stout body and the unique form of its caudal ramus.

Xarifia brevicauda n. sp.
Figs. 114–132

Type material.—5 females and 1 male from *Alveopora* sp. in 3.5 m, Nosy N'Tangam, on the western side of Nosy Bé, Madagascar. Collected October 23, 1964. Holotype female, allotype, and 3 paratypic females deposited in the United States National Museum; the remaining paratypic female (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 114 and 115) moderately slender, about 5.5 times longer than wide. Length 1.27 mm (1.23–1.35 mm) and greatest width 0.23 mm (0.22–0.23 mm), based on 5 specimens. External segmentation weakly indicated. Region dorsal to fifth legs with three nearly equal long posteriorly directed processes. Genital and postgenital segments fused (Fig. 116), form a short "tail," shield-shaped in dorsal view and only about one-sixth of total body length. Areas of attachment of egg sacs situated dorsally. Each sac (Fig. 115) 230×140 μ, containing two eggs, each about 140×120 μ. Caudal ramus (Fig. 117) elongated, 62×23 μ, with one outer marginal and four terminal setae. Body surface with a few scattered small hairs.

Rostral area (Fig. 118) tongue-shaped and rounded. First antenna (Fig. 119) 4-segmented (the third segment in other species being here divided into two segments) and elongated, about 75 μ in length. Setae long and naked. Armature: 3, 22 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna (Fig. 120) slender, 4-segmented, and armed as in previous five species. Terminal claw 28 μ long and slender, adjacent seta 18 μ; two setules near base of claw.

Labrum (Fig. 121) projected posteriorly at both free corners. Mandible (Fig. 121) with a pointed smooth blade. Paragnath not seen. First maxilla (Fig. 121) a small lobe with two setae. Second maxilla (Fig. 121) 2-segmented, second segment with two setae and a terminal lamellate expansion. Maxilliped (Fig. 122) probably 3-segmented. First segment with an outer distal expansion. Second segment with two inner setae and two expansions, one inner and the other distal. Third segment with a small lobe and a short terminal claw. Relationships of head appendages as in Figure 123.

Legs 1–4 with 3-segmented exopods and 2-segmented endopods. Spine and setal formula as follows:

P_1 and P_2 protopod	0–0;	1–0	
exp	I–0;	I–0;	I, 3
end	0–0;	2	
P_3 and P_4 protopod	0–0;	1–0	
exp	I–0;	I–0;	I, 2
end	0–0;	0	

In all four legs, basis with an outer seta and an inner group of hairs. Terminal claw on exopods unusually long, nearly as long as second and third segments combined. Endopods of legs 1 (Fig. 124) and 2 with second segment truncated terminally and bearing two setae; endopods of legs 3 (Fig. 125) and 4 with second segment rounded and without setae. In endopods of all four legs inner margin of first segment with hairs; outer margins of both segments with slender setules. Intercoxal plate of leg 1 broadly U-shaped, those of succeeding legs narrower.

Leg 5 (Fig. 126) elongated, 138 μ long, tapered distally, and bearing two unequal terminal setae 17 and 34 μ in length. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish orange, eye red, egg sacs dark gray.

Male.—The description of the male which follows is based on a single specimen, the allotype, which was studied in lactic acid without dissection.

Body (Figs. 127 and 128) moderately slender, about 8 times longer than wide, longer than female. Length 1.51 mm and greatest width 0.18 mm. External segmentation only weakly indicated. Caudal ramus (Fig. 129) minute, 20×13 μ, with four setae. Genital and postgenital segments together about one-fifth of total body length.

Rostral area as in female. First antenna like that of female but with an aesthete added on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath not seen. Maxilliped (Fig. 130) segmented and armed as in five previous species. Second segment with two inner setae. Claw 62 μ along its axis, armed with the usual two setae. Concave inner proximal margin with a rounded serrated excrescence and tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 131) minute, with only

a slight ridge bearing two setae representing the free segment. Leg 6 (Fig. 132) the usual posteroventral flap on genital segment bearing two setae.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *brevicauda*, from the Latin words *brevis* = short, and *cauda* = tail, refers to the unusually short genital and postgenital area.

Comparison with related species.—*X. brevicauda* may be distinguished from all previously described species in the genus by its abbreviated genital and postgenital region and by the serrated excrescence on the claw of the male maxilliped. Apart from these distinctions it may further be separated from those species having 2-segmented endopods in legs 1–4 (*X. dispar* Humes, 1962, *X. comata* Humes, 1962, *X. diminuta* Humes and Ho, 1967, *X. lamellispinosa*, and *X. decorata*) by the nature of the three outer spines on the exopods of legs 1–4 (the two proximal spines being short, the terminal spine longer than the last segment of the exopod).

Xarifia temnura n. sp.

Figs. 133–153

Type material.—12 females and 4 males from *Montipora sinensis* Bernard in a depth of 1 m, Nosy Taolankena, a small island on the northwestern side of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 11 paratypes (8 females and 2 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 133 and 134) elongated and very slender, about 10 times longer than wide. Length 1.52 mm (1.47–1.65 mm) and greatest width 0.15 mm (0.14–0.15 mm), based on 10 specimens. External segmentation lacking. Region dorsal to fifth legs smooth, without processes. Area bearing these legs turned ventrally (Fig. 135) toward sites of attachment of egg sacs and partially overlapping these regions of attachment laterally, thus producing a truncated appearance. Postgenital segments completely fused into a single body region which is relatively minute (52 μ along its dorsal surface and 83 μ along its ventral surface, not including the caudal rami). This "tail" region, together with the caudal rami, only about one-thirteenth of total body length. Caudal ramus (Fig. 136) fused with anal segment, lobate, 28 μ long with four short naked setae. Egg sac (Fig. 133) elongated, with 3 or 4 eggs in a row. In the female figured, right sac 430 μ long with middle egg 140 × 114 μ, left sac 506 μ long with penultimate egg 130 × 125 μ. Body surface with very few small hairs.

Rostral area (Fig. 139) weakly developed. First antenna (Fig. 137) 3-segmented and very short, about 23 μ long. Setae hyaline and naked. Armature: 3, 15 + 1 aesthete, and 6 + 2 aesthetes (though setae so densely arranged that it is difficult to count exact number). Second antenna (Fig. 138) 4-segmented and armed as in six previous species. Terminal claw transformed to a relatively long spine (28 μ in length); adjacent seta short (4 μ) and spiniform. A few small spines on anterior edge of second and third segments.

Labrum (Fig. 139) very slightly trilobed. Mandible (Fig. 140) with a pointed smooth blade. Paragnath (Fig. 139) consisting of a very small lobe with a few minute hairs. First maxilla (Fig. 141) a minute lobe with two naked setae. Second maxilla (Fig. 142) 2-segmented, second segment bearing two minute setae and a terminal clawlike spine. Maxilliped (Fig. 143) highly modified, with two inner setae on second segment and two smaller setae on what is probably the third segment. Relationships of head appendages as in Figure 139.

Legs 1–4 small, exopod of leg 1 (Fig. 144) 3-segmented, exopods of legs 2 (Fig. 146), 3, and 4 probably 3-segmented, but second and third segments of these legs without distinct line of separation; endo-

pods of all four legs 1-segmented. Spine and setal formula as follows:

P_1	protopod	0–0;	1–0	exp I–0; I–0; I, 3 end 1
P_2	protopod	0–0;	1–0	exp I–0; 0–0; I, 3 end 1
P_3 and P_4	protopod	0–0;	1–0	exp I–0; 0–0; I, 2 end 0

In all four legs, basis with an outer seta. Endopods of legs 1 (Fig. 145) and 2 (Fig. 146) with a single terminal seta; endopods of legs 3 (Fig. 147) and 4 without a seta. In all four endopods outer margin with numerous slender setules. Intercoxal plate of leg 1 U-shaped, becoming narrower in succeeding legs.

Leg 5 (Figs. 135 and 148) minute, located dorsolaterally above truncated region. Free segment reduced to a small lobe about 5 μ in length bearing two setae. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red, egg sacs reddish brown.

Male.—Body (Figs. 149 and 150) very slender, about 10.5 times longer than wide. Length 1.46 mm (1.43–1.50 mm) and greatest width 0.14 mm (0.13–0.15 mm), based on 4 specimens. External segmentation weakly indicated. Caudal ramus (Fig. 151) minute, 13 μ long, fused with anal segment and bearing four setae; the two rami rather divergent. Genital and postgenital segments together about one-third of total body length. Body surface with very few scattered small hairs.

Rostral area as in female. First antenna like that of female but an aesthete added on second segment. Second antenna as in female. Labrum (Fig. 152) resembling that of female but with posterior margin having a pair of small teeth medially and a small tooth at each corner. Mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 153) segmented and armed as in six previous species. Second segment with two inner setae. Claw 42 μ along its axis, armed with two setae. Concave margin proximally with a rather triangular serrated process; tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 150) very reduced, consisting only of three small setae, as in *X. lissa*. Leg 6 (Fig. 150) a posteroventral flap on genital segment bearing two small setae.

Spermatophore (seen only inside male, as in Figure 149) elongated.

Color in life as in female.

Etymology.—The specific name *temnura*, from the Greek words τέμνω = cut off and οὐρά = tail, refers to the truncated appearance of the posterior part of the body.

Comparison with related species.—The females of *X. temnura* may be recognized by the unique truncated posterior region and the very small postgenital area. In only three other species does the female lack processes on the region dorsal to the fifth legs. These are *X. reducta* Humes, 1962, *X. serrata* Humes, 1962, and *X. lissa*. All differ from *X. temnura*, however, in the body being much stouter (6–7 times longer than wide) and in the much longer fifth legs (*X. reducta* = 34 μ, *X. serrata* = 122 μ, and *X. lissa* = 72 μ). The male of *X. temnura* differs from all other species having 1-segmented endopods on legs 1–4 in the nature of the claw of the maxilliped and in the form of the caudal ramus.

Xarifia anomala n. sp.
Figs. 154–173

Type material.—2 females and 3 males from *Acropora palifera* (Lamarck) in a depth of 2 m, Tany Kely, a small island to the south of Nosy Bé, Madagascar. Collected October 3, 1963. Holotype female, allotype, and 1 male paratype deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 154 and 155) moderately slender, about 7.8 times longer than wide. Length 1.25 mm (1.25–1.26 mm) and greatest width 0.16 mm (0.16–0.17 mm), based on 2 specimens. External segmentation very weakly indicated. Re-

gion dorsal to fifth legs with three moderately long posteriorly directed processes, all nearly equal in length. Genital and postgenital region recurved in specimens in alcohol, with caudal rami turned dorsally (Fig. 156), this entire region comprising about one-fifth of total body length. Areas of attachment of egg sacs located dorsolaterally. Egg sac unknown. Caudal ramus (Fig. 157) elongated, 52 × 15 μ, with one outer marginal and four terminal naked setae. Body surface with a few scattered small hairs.

Rostral area forming a prominent rounded lobe (Fig. 161), similar to that of male (Fig. 168). First antenna small, about 33 μ in length, probably 3-segmented, though last two segments seem partially divided; similar to that of male (Fig. 168). Armature: 3, 22 (no aesthete visible here), and 9 + 2 aesthetes. Second antenna (Fig. 158) 4-segmented and armed as in previous seven species. Terminal claw recurved and slender, 10 μ long, with adjacent seta 19 μ in length.

Labrum of a form similar to that of male (Fig. 169). Mandible a smooth attenuated recurved blade as in male (Fig. 170). Paragnath an obscure minute smooth prominence near inner base of first maxilla. First maxilla (Fig. 159) a small lobe with two setae and a small spinous process. Second maxilla 2-segmented, second segment with two small setae and an elongated lamellate expansion, as in male (Fig. 171). Maxilliped (Fig. 160) probably 3-segmented. First segment with a well sclerotized almost hooklike lobe on distal outer surface. Second segment with two inner setae. Third segment with a spiniform process and a terminal lamellate element. Relationships of head appendages as in Fig. 161.

Legs 1–4 with 3-segmented exopods and 2-segmented endopods. Spine and setal formula as follows:

P_1	protopod 0–0; 1–0	exp I–0; I–0; I, 3	
		end 0–0; 0	
P_2	protopod 0–0; 1–0	exp I–0; I–0; I, 2	
		end 0–0; 3	
P_3 and P_4	protopod 0–0; 1–0	exp I–0; I–0; I, 2	
		end 0–0; 0	

In all four legs intercoxal plates narrow and V-shaped; basis with an outer seta and an inner group of hairs. Claws on exopods with short but conspicuous terminal lamellae. Second segment of endopod of leg 1 (Fig. 162) without terminal setae (though slender setules occur along outer margin of segment). Second segment of endopod of leg 2 (Fig. 163) with three terminal setae. Legs 3 and 4 resembling in general structure first two legs, but second endopod segment without terminal setae.

Leg 5 (Fig. 164) elongated, about 100 μ in length, tapered distally, with two unequal terminal setae 13 and 23 μ long. Leg 6 absent.

Color in life unknown.

Male.—Body (Figs. 165 and 166) fairly slender, about 9 times longer than wide. Length 1.21 mm (1.15–1.25 mm) and greatest width 0.13 mm (0.12–0.14 mm), based on 3 specimens. External segmentation very weak. Genital and postgenital segments together about one-fourth of total body length. Caudal ramus (Fig. 167) reduced to five setae arising directly from anal segment.

Rostral area and first antenna (Fig. 168) like those in female, as far as could be determined. (The presence of an extra aesthete in the male, as often found in this genus, could not be established.) Second antenna as in female. Labrum (Fig. 169), mandible (Fig. 170), paragnath, first maxilla, and second maxilla (Fig. 171) resembling those of female. Maxilliped (Fig. 172) segmented and armed as in seven previous species. Second segment with two unequal inner setae. Claw 28 μ along its axis, armed with two setae. Concave margin with a few spinules and tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 173) consisting of three small setae, arising from body wall and without a free segment. Leg 6 (Fig. 173) the usual posteroventral flap on genital segment with two small setae.

Spermatophore seen only inside body of male, as in Figure 173.

Color in life unknown.

Etymology.—The specific name *anomala*, from ἀνώμαλος = uneven or unequal, refers to the peculiar formula for the terminal armature of the endopods of legs 1–4.

Comparison with related species.—*X. anomala* may be distinguished from the six already described species of *Xarifia* which have 2-segmented endopods on legs 1–4 by the absence of terminal setae on the endopod of its first leg and by the extreme sexual dimorphism in the caudal ramus. Three of these six species, *X. dispar* Humes, 1962, *X. comata* Humes, 1962, and *X. decorata*, have the outer spine on the second segment of the exopod of leg 1 reduced or absent, thus further separating them from the new species. Of the remaining three species, *X. brevicauda* has a shorter postgenital region, *X. lamellispinosa* has a short stout claw on the second antenna and a toothed mandible, and *X. diminuta* Humes and Ho, 1967, has relatively short stout spines on the exopods of legs 1–4.

Xarifia hamata n. sp.

Figs. 174–194

Type material.—64 females and 16 males from *Turbinaria* sp. (tabulate group, near *T. elegans* Bernard but not this species) in a depth of 2 m, Nosy Taolankena, a small island off the northwestern shore of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 58 paratypes (45 females and 13 males) deposited in the United States National Museum; 11 paratypic females in the Museum of Comparative Zoology; and the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 174 and 175) moderately slender, about 6.3 times longer than wide. Length 1.38 mm (1.29–1.42 mm) and greatest width 0.22 mm (0.21–0.22 mm), based on 10 specimens. External segmentation weakly indicated, except in a few specimens where postgenital segments are more clearly delimited (Fig. 176). Region dorsal to fifth legs with three moderately long posteriorly directed processes, all nearly equal in length. Genital and postgenital region short and held at a slight angle to main body axis, this region comprising about one-seventh of total body length. Areas of attachment of egg sacs situated dorsolaterally. Egg sac (Fig. 175) about 374 × 198 μ, containing usually 5, but sometimes 6 eggs, each about 115 μ in diameter. Caudal ramus (Fig. 177) not clearly delimited from anal segment, approximately 41 × 17 μ (width taken at middle), with a strong outer marginal seta and four more slender terminal setae. All setae naked. Dorsal surface of ramus with a few hairs. Body surface ornamented with very few minute hairs.

Rostral area resembling that of *X. lamellispinosa*. First antenna (Fig. 178) small, about 55 μ in length, apparently 3-segmented, though second and third segments show partial division. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes. Second antenna (Fig. 179) 4-segmented and armed as in eight previous species. Last segment terminally with a slender claw 13 μ long, a seta 19 μ, a small setule, and a minute spinous process.

Labrum (Fig. 180) with trilobate free margin. Mandible (Fig. 181) with a sinuous smooth attenuated blade. Paragnath a small lobe with a few hairs, similar to that shown for the male in Figure 193. First maxilla (Fig. 182) with two naked setae and a spinous process. Second maxilla (Fig. 183) 2-segmented, second segment elongated with two proximal inner setae and a third seta near its obtuse hyaline tip. Maxilliped (Fig. 184) 3-segmented, second segment with two inner setae, third with two inner setae and terminating in a clawlike process. Relationships of head appendages as in Figure 185.

Legs 1–4 with similar form and segmentation, exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1	protopod	0–0; 1–0	exp I–0; 1–0; I, 3
			end 0–0; 2
P_2	protopod	0–0; 1–0	exp I–0; 1–0; I, 3
			end 0–0; 1, I
P_3 and P_4	protopod	0–0; 1–0	exp I–0; 1–0; I, 2
			end 0–0; I

First segment of exopod of all four legs with a spiniform process at base of outer spine; second segment of these exopods with an outer seta instead of a spine. In all four legs inner margins of first and second segments of exopods and outer margins of both segments of endopods with long hairs. Terminal segment of endopod of leg 1 with two setae (Fig. 186), of leg 2 with an outer seta and an inner clawlike spine (Fig. 187), and of legs 3 and 4 with a single clawlike spine (Fig. 188). Leg 4 (not drawn) similar to leg 3. Intercoxal plates roughly V-shaped in all four legs.

Leg 5 (Fig. 189) moderately elongated, about 58 μ long, tapered distally, with two unequal terminal setae 24 and 32 μ long. Leg 6 absent.

Color in life in transmitted light slightly brownish, intestine reddish brown, eye red, egg sacs reddish brown to dark grayish black.

Male.—Body (Figs. 190 and 191) slender, about 9.1 times longer than wide. Length 1.28 mm (1.15–1.56 mm) and greatest width 0.14 mm (0.13–0.14 mm), based on 10 specimens. External segmentation weakly defined except in some specimens in postgenital area (Fig. 192). Genital and postgenital segments together less than one-third of total body length. Caudal ramus similar to that of female but smaller and relatively broader, 25 × 13 μ.

Rostral area as in female. First antenna like that of female, but with four aesthetes, one being added on midanterior margin of middle segment. Second antenna as in female. Labrum resembling that of female but with a minute toothlike process on corners of outer lobes. Mandible, paragnath (Fig. 193), first maxilla, and second maxilla as in female. Maxilliped (Fig. 194) segmented and armed as in eight previous species. Second segment with two inner setae. Claw 40 μ along its axis, armed with two setae. Concave margin with a few minute serrations near distal seta.

Legs 1–4 segmented and armed as in female. Leg 5 without a free segment, consisting of three small setae, two of them arising from a very slight ridge (Fig. 192). Leg 6 the usual posteroventral flap on genital segment bearing two small setae (Fig. 192).

Spermatophore seen only inside body of male, as in Figure 192.

Color in life resembling that of female.

Etymology.—The specific name *hamata*, from Latin = provided with hooks, refers to the clawlike spines on the endopods of legs 2–4.

Comparison with related species.—*X. hamata* may be distinguished from all other nineteen species in the genus by the combination of the following three characters: the endopods in all four legs 2-segmented, the endopods of legs 3 and 4 with a clawlike terminal spine, and the exopods of all four legs with a spinal armature of I, 1, I. The presence of a clawlike spine on the second segment of the endopod in legs 2–4 is sufficient to separate the new species from all others in the genus (where the endopods either bear setae or are unarmed, though they may be ornamented with slender setules or hairs).

Xarifia dispar Humes, 1962

This species has been previously recorded only from *Echinopora carduus* Klunzinger in Madagascar. It is now reported from two new hosts as follows:

1) from *Echinopora gemmacea* (Lamarck): 3 females and 7 males in 2 m, northern end of Nosy Sakatia, off the western side of Nosy Bé, Madagascar, September 18, 1963; 6 females and 3 males in 1 m, Pte. de Tafondro, Nosy Bé, September 21, 1963.

2) from *Echinopora lamellosa* (Esper): 6 females and 7 males in 1 m, Pte. Ambar-

ionaomby, Nosy Komba, near Nosy Bé, June 24, 1963.

The specimens from the two new hosts agree in all significant features with paratypic specimens. Although in the original description paragnaths were said to be absent, we have found both in paratypic specimens and in the new material two small elongated lobes which are clearly paragnaths.

Xarifia serrata Humes, 1962

The type specimens of this species were taken by Humes (1962) in Madagascar from *Pocillopora damicornis* Dana. He found other specimens on *Seriatopora subseriata* Ehrenberg and *Pocillopora verrucosa* (Ellis and Solander). The species was again reported from *Seriatopora subseriata* by Humes and Frost (1964).

We have now recovered it from a new host, *Pocillopora bulbosa* Ehrenberg, from which 29 females and 34 males were taken in 10 cm at Ankify, on the mainland of Madagascar opposite Nosy Komba, June 11, 1964. These specimens agree completely with paratypic material.

ORSTOMELLA n. gen.

Type species.—*Orstomella faviae* n. sp.

Female.—Body elongated, slender, with indistinct segmentation. Region dorsal to fifth legs without processes. Rostral area weakly developed. Caudal ramus with a few short terminal setae.

First antenna 6-segmented, first segment with an anterior process, remaining segments with numerous short setae. Second antenna 3-segmented, terminal segment (with slight indication of division into two segments) bearing two unequal elements.

Labrum with widely separated lobes. Mandible and paragnath absent. First maxilla with three elements. Second maxilla 2-segmented. Maxilliped 3-segmented.

Legs 1 and 2 with 2-segmented exopods and endopods. Legs 3 and 4 with 2-segmented exopods, but endopods absent. Leg 5 a ridge with three setae. Leg 6 absent.

Male.—Resembling female with following exceptions. First antenna with four aesthetes. Lateral margins of labral lobes with crenated depressions. First maxilla with two elements. Maxilliped probably 4-segmented, claw short. Leg 6 a posteroventral flap with two very small setae.

Living in polyps of madreporarian corals.

Gender feminine.

Etymology.—The name *Orstomella* is formed from ORSTOM, the abbreviation for the Office de la Recherche Scientifique et Technique Outre-Mer, the organization of the French Government which operates the Centre O.R.S.T.O.M. (formerly the Centre d'Océanographie et des Pêches) at Nosy Bé, Madagascar, and which has aided in so many ways the field work in connection with this study.

Orstomella faviae n. sp.

Figs. 195–219

Type material.—11 females, 8 males, and 4 copepodids from two colonies of *Favia* sp. in a depth of 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected April 10, 1964. Holotype female, allotype, and 12 paratypes (7 females and 5 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 195 and 196) elongated and slender, about 6.4 times longer than wide, slightly thickened dorsoventrally in prosomal region, with indistinct segmentation and lacking fine ornamentation. Length 2.19 mm (2.10–2.26 mm) and greatest width 0.34 mm (0.32–0.36 mm), based on 10 specimens. Region dorsal to fifth legs without processes. Genital and postgenital segments together about one-third of total body length. Genital segment (Fig. 197) bipartite, the anterior third narrow (78 × 179 μ) with areas of attachment of egg sacs dorsolateral in position, the posterior two-thirds broader (177 × 198 μ). Three postgenital segments 133 × 180, 55 × 144, and 107 × 122 μ from anterior to posterior. Last segment with a prominent anal

operculum. Caudal ramus (Fig. 198) moderately elongated, 80 × 26 μ, about 3 times longer than wide; bearing terminally a seta 20 μ and a minute spinule 3 μ long, and having on its proximal outer margin a hyaline setule 6 μ long. Egg sac unknown.

Rostral area (Fig. 199) weakly developed. First antenna (Fig. 199) short, about 80 μ in length, and 6-segmented, bearing numerous short setae which are sclerotized proximally but hyaline distally with somewhat obtuse tips. Lengths of segments (measured along their posterior non-setiferous margins) 15, 24, 14, 9, 9, and 8 μ respectively. First segment with an anterior process (probably not a true element, since it has no articulation). Formula for armature: 0, 3, 6, 4, 3, 6. A few minute spinules on surface of segments. Second antenna (Fig. 200) 3-segmented, about 44 μ long without setae; first segment wide with an anteroventral jointed seta 16 μ long; second segment elongated, slender, and unarmed; third segment also elongated and slender, with slight indication of division and bearing terminally a jointed seta 15 μ and a short spine 5 μ long.

Labrum (Fig. 201) with two lobes widely separated and both bearing a surficial seta; other fine ornamentation as indicated in figure. Mandible and paragnath absent. First maxilla (Fig. 202) a small lobe with three distally hyaline elements, two of them bipartite as shown in figure. Second maxilla (Fig. 203) 2-segmented, first segment large and unarmed, second small, bearing two hyaline obtuse elements and a spinous process and prolonged terminally as a rather obtuse process with hyaline border (cf. Figures 203 and 204). Maxilliped (Fig. 205) apparently 3-segmented; first segment unarmed; second segment indistinctly separated from third and bearing two short elements, one straight, the other recurved; third segment small, armed with one hyaline obtuse element and having a terminal prolongation with hyaline lamellae. Labrum and mouthparts situated close together (Fig. 206) with a small median ventral lobe (see Figure 201) between the second maxillae and maxillipeds.

Leg 1 (Fig. 207) and leg 2 with 2-segmented exopods and endopods. Leg 3 (Fig. 209) and leg 4 with 2-segmented exopods, but without endopods. Spine and setal formula as follows:

P_1 and P_2	protopod 0–0;	1–0	exp I–0; (I), I end 0–0; 1
P_3 and P_4	protopod 0–0;	1–0	exp I–0; I, I end –

Low median ventral protuberances in front and behind first three pairs of legs (seen in lateral view in Figure 196).

In leg 1, first segment of exopod with a small outer spine, second segment with a minute outer spine (or spinous process ?) and a terminal clawlike spine which is swollen on its concave edge (Fig. 208). Endopod with first segment unarmed, second segment with a single partly hyaline and obtusely tipped terminal seta and a small hyaline lobe. Leg 2 similar to leg 1.

In leg 3 both segments of exopod with a small outer spine and second segment with terminal clawlike spine having hyaline lamellae (cf. Figures 209 and 210). Endopod absent. Leg 4 similar to leg 3.

Leg 5 (Fig. 211) consisting of a low slightly sclerotized ridge with three obtuse and mostly hyaline setae 9, 13, and 8 μ in length. Position of this leg as in Figure 196.

Leg 6 absent.

Color in life in transmitted light bright red, with eye darker red.

Male.—Body (Figs. 212 and 213) resembling that of female, about 7.6 times longer than wide. Length 2.12 mm (1.99–2.24 mm) and greatest width 0.28 mm (0.23–0.34 mm), based on 8 specimens. Genital and postgenital segments together about one-third of total body length. Genital segment (Fig. 214) wider than long, 138 × 256 μ. Four postgenital segments 185 × 216, 143 × 190, 65 × 143, and 104 × 122 μ from anterior to posterior. Caudal ramus as in female, but slightly longer, 91 × 23 μ, with the large terminal seta 23 μ long.

Rostral area as in female. First antenna

(Fig. 215) segmented and armed as in female, except for three aesthetes being added on segment 3 and one aesthete on segment 4, making the formula 0, 3, 6 + 3 aesthetes, 4 + 1 aesthete, 3, and 6. Second antenna as in female.

Labrum (Fig. 216) with two lobes smaller than in female and having lateral depressions with well sclerotized crenated edges. Mandible and paragnath absent. First maxilla (Fig. 217) a small lobe with only two elements. Second maxilla as in female. Maxilliped (Figs. 218 and 219) probably 4-segmented, but segmentation obscure. First segment unarmed, second large with two inner hyaline setae, third small and unarmed. Fourth segment forming a short terminal blunt claw 19 μ in length bearing two unequal elements. Relationships of mouthparts as in female.

Legs 1–4 as in female.

Leg 5 similar to that of female.

Leg 6 (Fig. 214) consisting of a posteroventral flap on genital segment bearing two minute setae 8 and 6 μ long.

Spermatophore seen only inside body of male, as in Figure 213.

Color in life as in female.

Etymology.—The specific name *faviae* is derived from the generic name of the host.

Orstomella lobophylliae n. sp.
Figs. 220–239

Type material.—10 females and 16 males from *Lobophyllia costata* (Dana) in a depth of 6–8 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected December 28, 1963. Holotype female, allotype, and 20 paratypes (7 females and 13 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimen.—1 female from *Lobophyllia corymbosa* (Forskål) in 1 m, Ambariobe, January 13, 1964.

Female.—Body (Figs. 220 and 221) in general appearance similar to preceding species, but much smaller, about 5.5 times longer than wide. Length 1.20 mm (1.23–1.39 mm) and greatest width 0.22 mm (0.17–0.24 mm), based on 9 specimens. Region dorsal to fifth legs without processes. Genital and postgenital segments together about four-tenths of total body length. Genital segment (Fig. 222) bipartite, the anterior half 70 × 140 μ, relatively not as narrow as in preceding species, with areas of attachment of egg sacs lateral in position; the posterior half 101 × 127 μ. Three postgenital segments 90 × 102, 40 × 80, and 44 × 78 μ from anterior to posterior. Last segment with a prominent anal operculum. Caudal ramus (Fig. 223) short, 26 × 15 μ, nearly two times longer than wide, bearing terminally two setae 18 and 11 μ and a minute spinule 3 μ long, and having on its proximal outer margin a hyaline setule 10 μ long. Egg sac unknown.

Rostral area (Fig. 224) not well developed. First antenna (Fig. 224) short, about 84 μ in length, and 6-segmented, bearing numerous short hyaline setae. Lengths of segments (measured along their posterior non-setiferous margins) 20, 24, 11, 10, 9, and 9 μ, respectively. First segment having an anterior process with recurved tip. Two setae on segment 2 and one on segment 3 modified, without evident articulation and with terminal flagella. Formula for armature: 0, 3, 6, 4, 3, 6. A few minute setules on surface of segments. Second antenna (Fig. 225) 3-segmented, short, only 27 μ long without the setae; first two segments unarmed, third segment (showing slight indication of division) with terminally a jointed seta 15 μ and a short spine 6 μ.

Labrum (Fig. 226) resembling that of previous species, but two lobes smaller. Mandible and paragnath absent. First maxilla (Fig. 227) similar to preceding species, with three terminal elements, but the two bipartite elements attenuated. Second maxilla (Fig. 228) similar to preceding species, but terminal prolongation of second segment setiform. Maxilliped (Fig. 229) resembling that of *O. faviae*. Labrum and

mouthparts held close together as in that species.

Leg 1 (Fig. 230) and leg 2 with 2-segmented exopods and endopods. Leg 3 (Fig. 231) and leg 4 with 2-segmented exopods, but without endopods. Spine and setal formula as follows:

P_1 and P_2	protopod	0–0; 1–0	exp I–0; (I), 1; I, 1
			end 0–0; 1
P_3 and P_4	protopod	0–0; 1–0	exp I–0; I, I
			end –

Low median ventral protuberances in front and behind first three pairs of legs (Fig. 221) as in *O. faviae*.

In leg 1 first segment of exopod with a small outer spine, second segment with a minute outer spine (or spinous process ?), a minute spinule, a terminal clawlike spine, and an inner setule. Endopod with first segment unarmed, second segment bearing a terminal seta, with nearby on anterior surface a minute setule and a small patch of denticles. Leg 2 similar to leg 1.

In leg 3 both segments of exopod with a small outer spine, and second segment with clawlike terminal spine having hyaline lamellae. Endopod absent. Leg 4 like leg 3, but second segment with minute outer spine smaller (Fig. 232).

Leg 5 (Fig. 233) consisting of a low ridge with three setae 10, 12, and 9 μ long, more attenuated than in *O. faviae*.

Leg 6 absent.

Color in life in transmitted light bright red, with eye darker red.

Male.—Body (Figs. 234 and 235) similar to that of the female, about 7 times longer than wide. Length 1.30 mm (1.20–1.45 mm) and greatest width 0.19 mm (0.16–0.23 mm), based on 10 specimens. Genital and postgenital segments together (Fig. 236) about one-third of total body length. Caudal ramus as in female but slightly larger, 29 × 16.5 μ.

Rostral area as in female. First antenna similar to that of female, but with four aesthetes added as in male of preceding species. Second antenna as in female.

Labrum (Fig. 237) with both lobes having a lateral depression with crenated edges. Mandible and paragnath absent. First maxilla (Fig. 238) with only two elements. Second maxilla as in female. Maxilliped (Fig. 239) resembling that of *O. faviae*, the terminal claw 17 μ long. Relationships of mouthparts as in female.

Legs 1–4 as in female.

Leg 5 similar to that of female.

Leg 6 (Fig. 236) a posteroventral flap on genital segment bearing two minute setae about 3 μ in length.

Spermatophore seen only inside body of male, as in Figure 235.

Color in life as in female.

Etymology.—The specific name *lobophylliae* is derived from the generic name of the host.

Comparison with the type species.—*Orstomella lobophylliae* differs in significant respects from *O. faviae*. It is much smaller (female 1.20, male 1.30 mm) than that species (female 2.19, male 2.12 mm). The caudal ramus of the female is shorter (26 × 15 μ, or about 2:1) than in *O. faviae* (80 × 26 μ, or about 3:1). There are three modified flagellated setae on the first antenna, while in *O. faviae* all the setae are similar. The first segment of the second antenna is unarmed, while in *O. faviae* this segment bears a jointed seta. In leg 5 the three setae are obtuse, but in *O. faviae* they are attenuated. Other minor differences exist in the armature of the mouthparts and in legs 1–4.

Relationship of Orstomella *with the hosts.*—Both *O. faviae* and *O. lobophylliae* evidently live in the polyps of the corals. Specimens were recovered in the sediment obtained after allowing the corals to remain overnight in alcoholized sea water (containing about 5 percent ethyl alcohol). They were never found after rinsing the freshly collected corals for only a few minutes. The copepods apparently are stimulated by the weak alcohol to emerge from the polyps, when they fall to the bottom of the container. Since the copepods are unable to swim, they are unable to regain

their positions in the coral after the effects of the alcohol diminish.

The taxonomic position of ORSTOMELLA.— In its elongated body form and its close association with corals, the genus *Orstomella* is suggestive of the genus *Xarifia* Humes, 1960.

There are, however, several important features which distinguish the two genera. In *Orstomella* the processes dorsal to the fifth legs in the female, characteristic of most *Xarifia*, are absent; the first antenna is clearly 6-segmented, instead of 3-segmented (with in some species a partial division of segments 2 and 3) as in *Xarifia*; the second antenna is 3-segmented (with slight indication of partial division of segment 3), instead of 4-segmented (3-segmented in *X. obesa* and a few others); the labrum shows marked sexual dimorphism, instead of weak dimorphism or none in *Xarifia*; the mandible and paragnath are absent, while in *Xarifia* there is a mandible in all species and a paragnath in some; the exopods of legs 1–4 are 2-segmented, instead of 3-segmented in *Xarifia*; and the endopods of legs 3 and 4 are absent, but present in *Xarifia*.

These differences might be regarded as sufficiently fundamental to justify placing *Orstomella* in a separate family. When, however, the range of variation within the genus *Xarifia* is considered, and the tendencies toward simplification and reduction exhibited by *Orstomella* are kept in mind, it seems unlikely to us that *Orstomella* truly represents a familial divergence. In certain species of *Xarifia*, for example, there are no processes dorsal to the fifth legs in the female, the second antenna is 3-segmented, the labrum shows weak sexual dimorphism, the mandible is reduced to a very minute blade, the paragnath may be absent, and the exopods of legs 1–4, though 3-segmented, may show a marked reduction of the second segment. The differences in the segmentation of the first antenna (6-segmented in *Orstomella*, 3-segmented with sometimes partial division of segments 2 and 3 in *Xarifia*) and the nature of the endopods of legs 3 and 4 (absent in *Orstomella*, 1- or 2-segmented in *Xarifia*) seem to be intrafamilial features. Differences of a similar degree exist within other poecilostome families, for example, the Lichomolgidae. The absence of a mandible in *Orstomella*, while of fundamental importance, may simply represent an extreme in intrafamilial reduction, a strong tendency toward reduction of this appendage being already seen in certain *Xarifia*.

For these reasons we place *Orstomella* provisionally in the Xarifiidae, along with the genus *Xarifia*. The study of further collections of related copepods from corals would undoubtedly clarify the relationships of these two genera.

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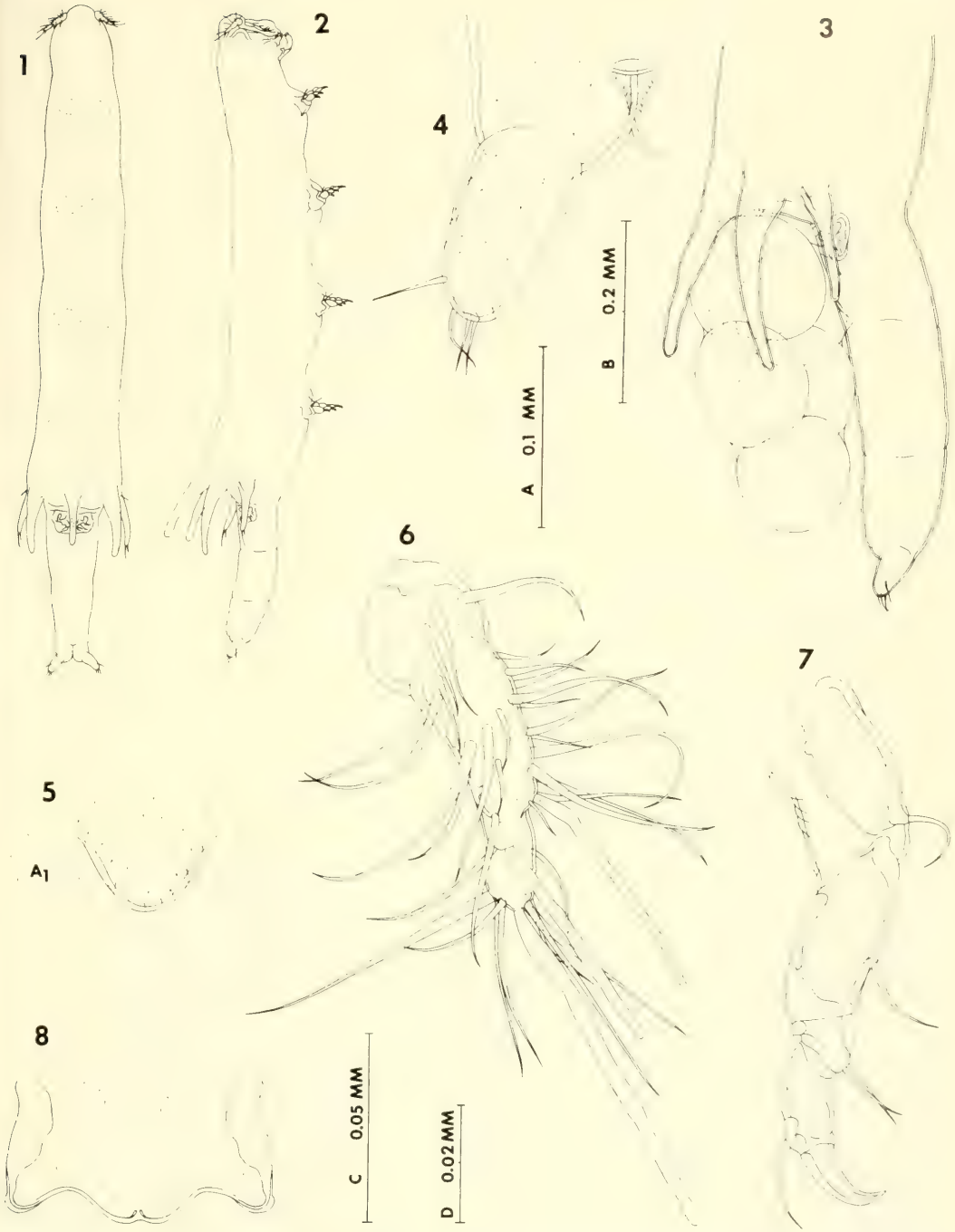
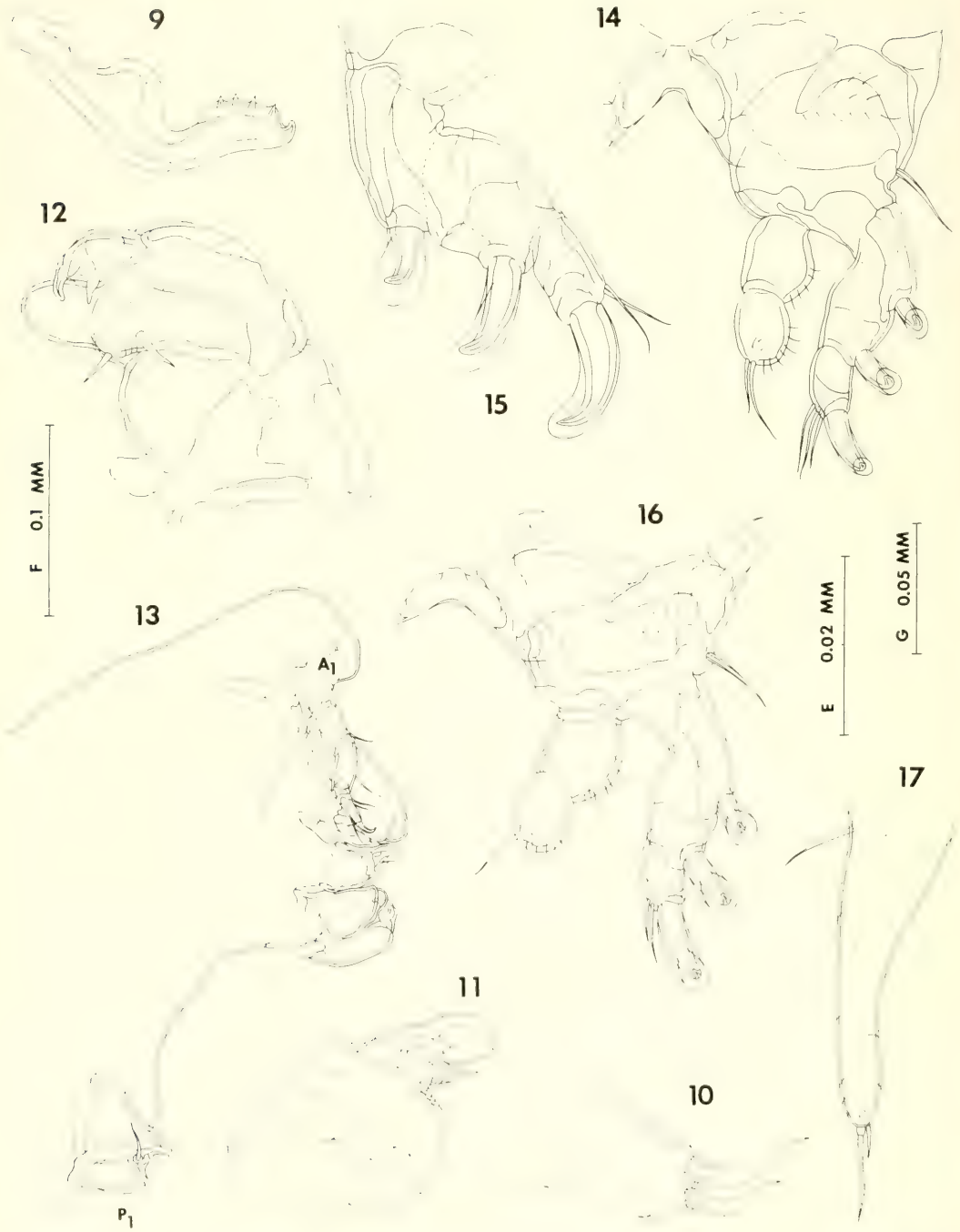
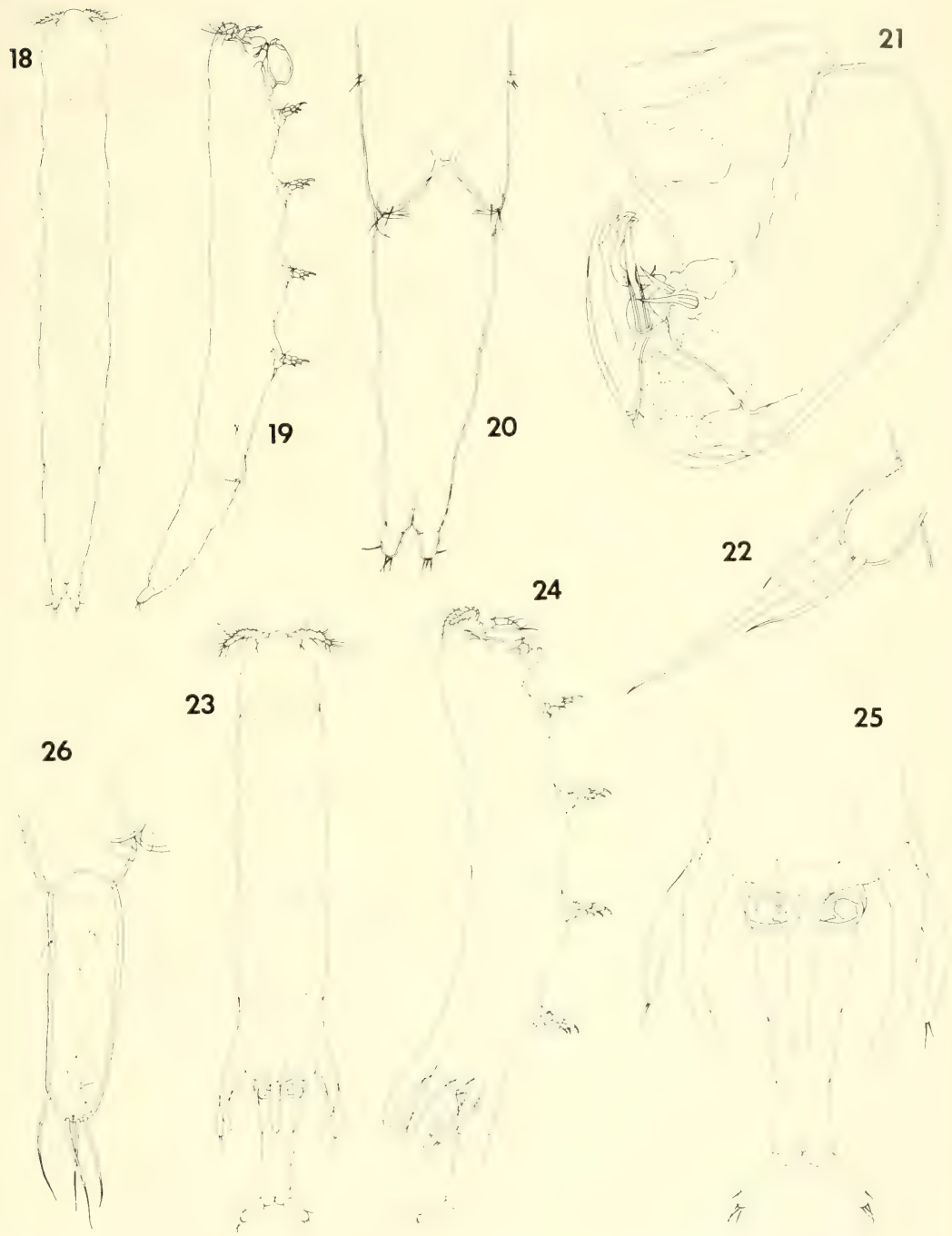
(*Received 8 March 1967.*



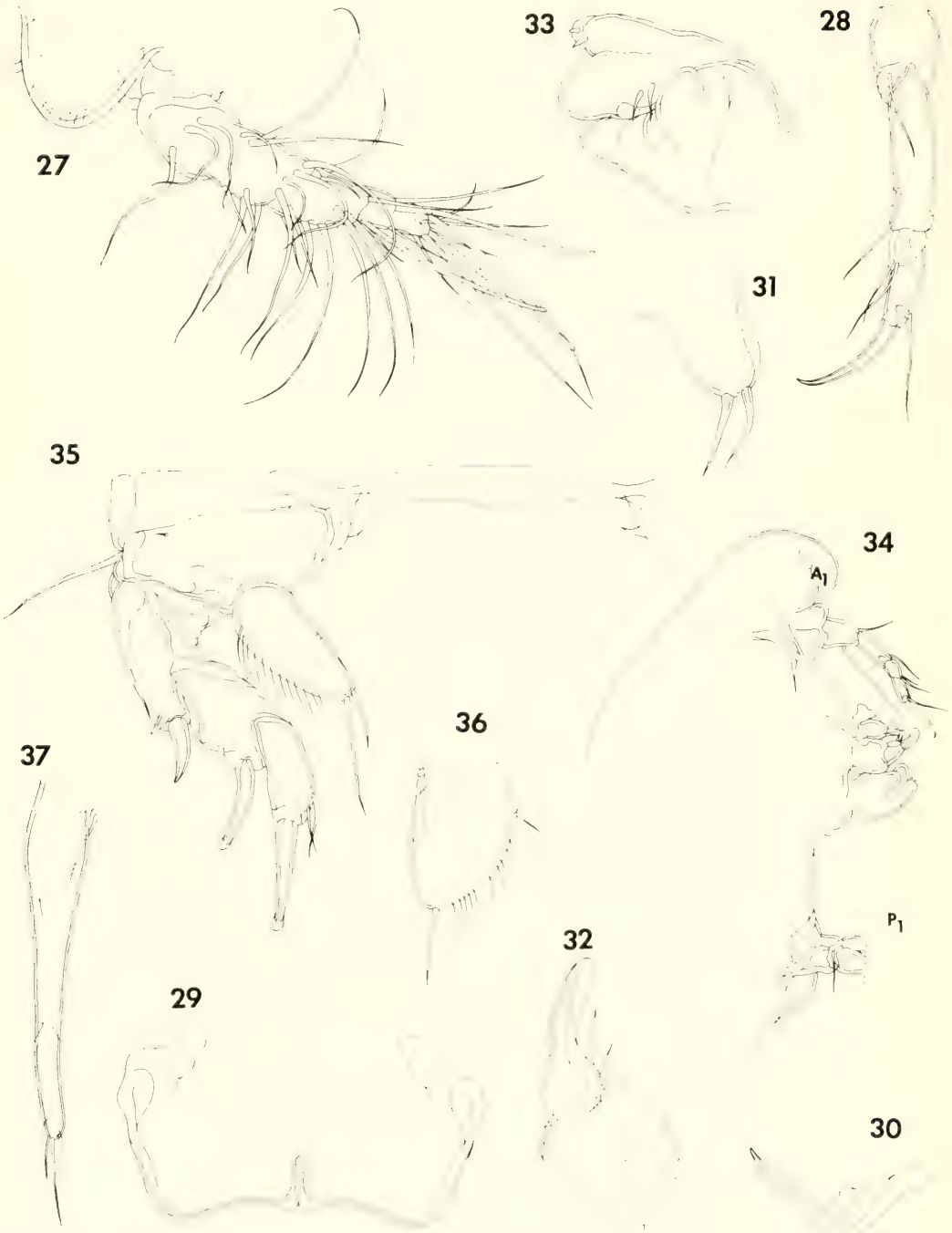
Figures 1–8. *Xarifia lamellispinosa* n. sp., female. 1, body, dorsal (A); 2, body, lateral (A); 3, posterior part of body and egg sac, lateral (B); 4, caudal ramus, dorsal (C); 5, rostrum, ventral (C); 6, first antenna, anterodorsal (D); 7, second antenna, ventral (D); 8, labrum, ventral (C).



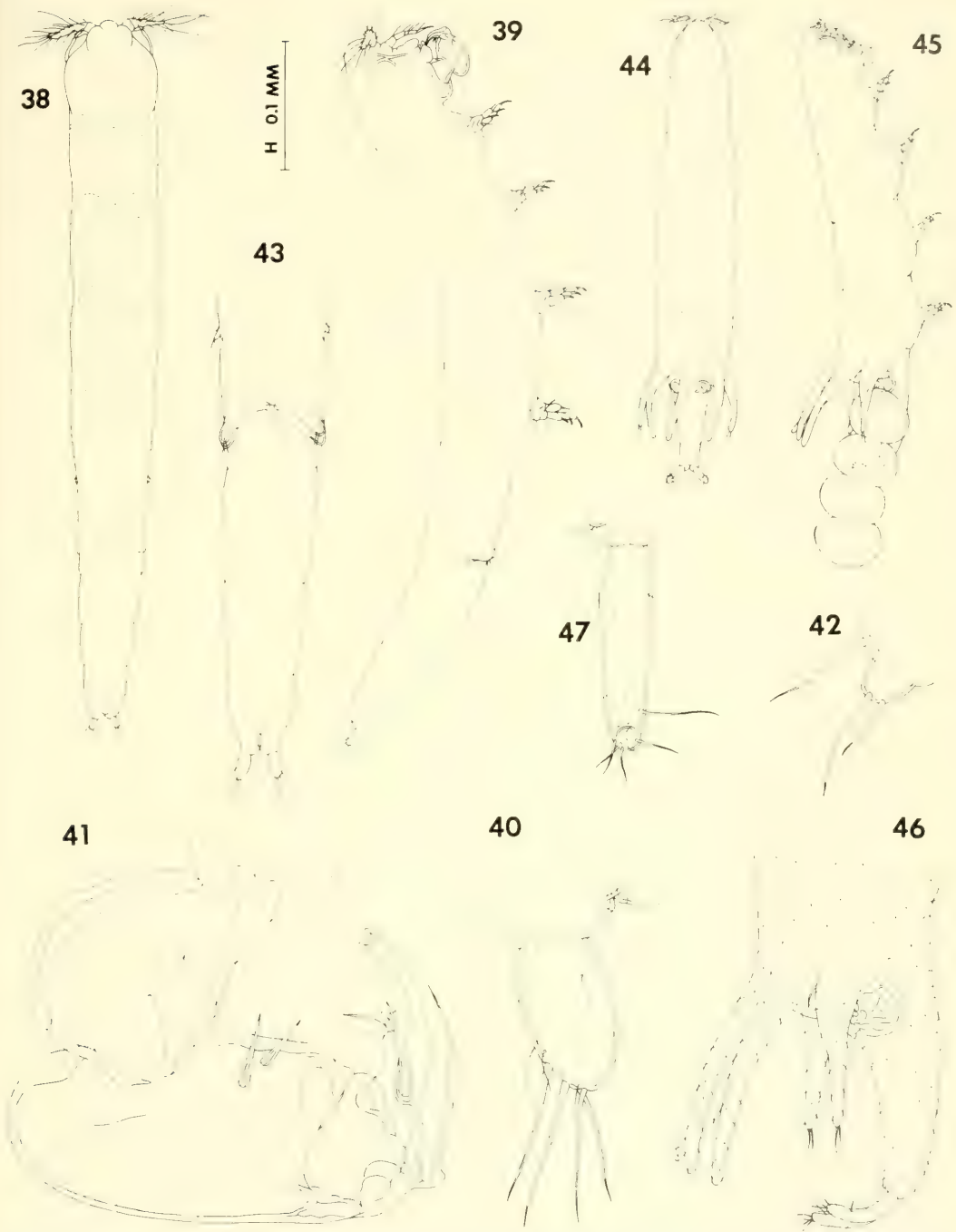
Figures 9–17. *Xarifia lamellispinosa* n. sp., female (continued). 9, mandible, dorsal (E); 10, first maxilla, dorsal (C); 11, second maxilla, anterior (D); 12, maxilliped, inner (D); 13, anterior part of body, lateral (F); 14, leg 1 and intercoxal plate, posterior (C); 15, exopod of leg 2, posterior (D); 16, leg 3 and intercoxal plate, posterior (C); 17, leg 5, lateral (G).



Figures 18–22. *Xarifia lamellispinosa* n. sp., male. 18, body, dorsal (A); 19, body, lateral (A); 20, urosome, ventral (B); 21, maxilliped, medial (C); 22, leg 5, ventral (E).
Figures 23–26. *Xarifia exigua* n. sp., female. 23, body, dorsal (B); 24, body, lateral (B); 25, urosome, dorsal (F); 26, caudal ramus, dorsal (D).

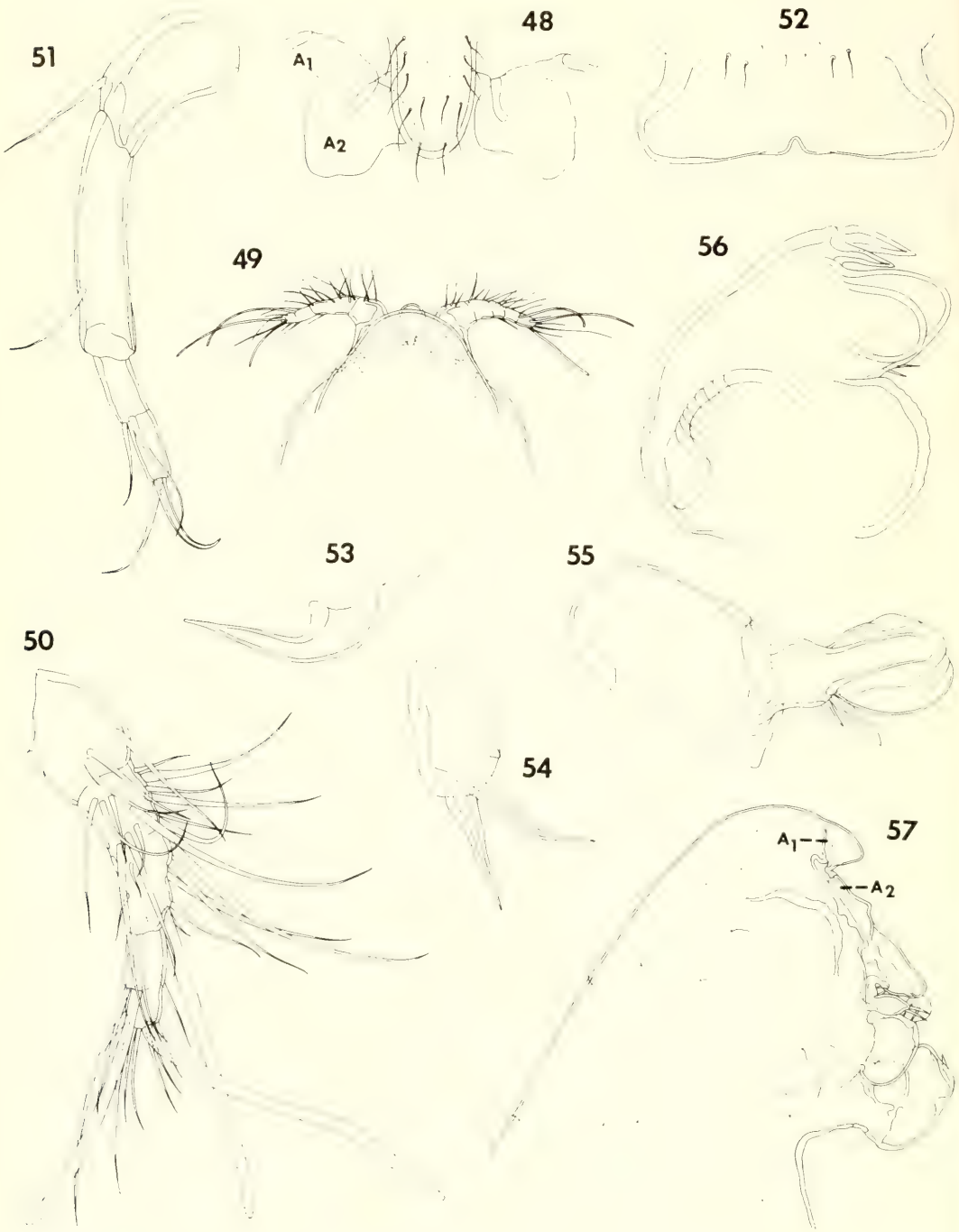


Figures 27–37. *Xarifia exigua* n. sp., female (continued). 27, rostrum and first antenna, anteroventral (D); 28, second antenna, ventral (D); 29, labrum, anteroventral (C); 30, mandible, anteroventral (E); 31, first maxilla, anteroventral (E); 32, second maxilla, anteroventral (E); 33, maxilliped, inner (E); 34, anterior part of body, lateral (G); 35, leg 1 and intercoxal plate, anterior (E); 36, endopod of leg 3, anterior (E); 37, leg 5, lateral (C).

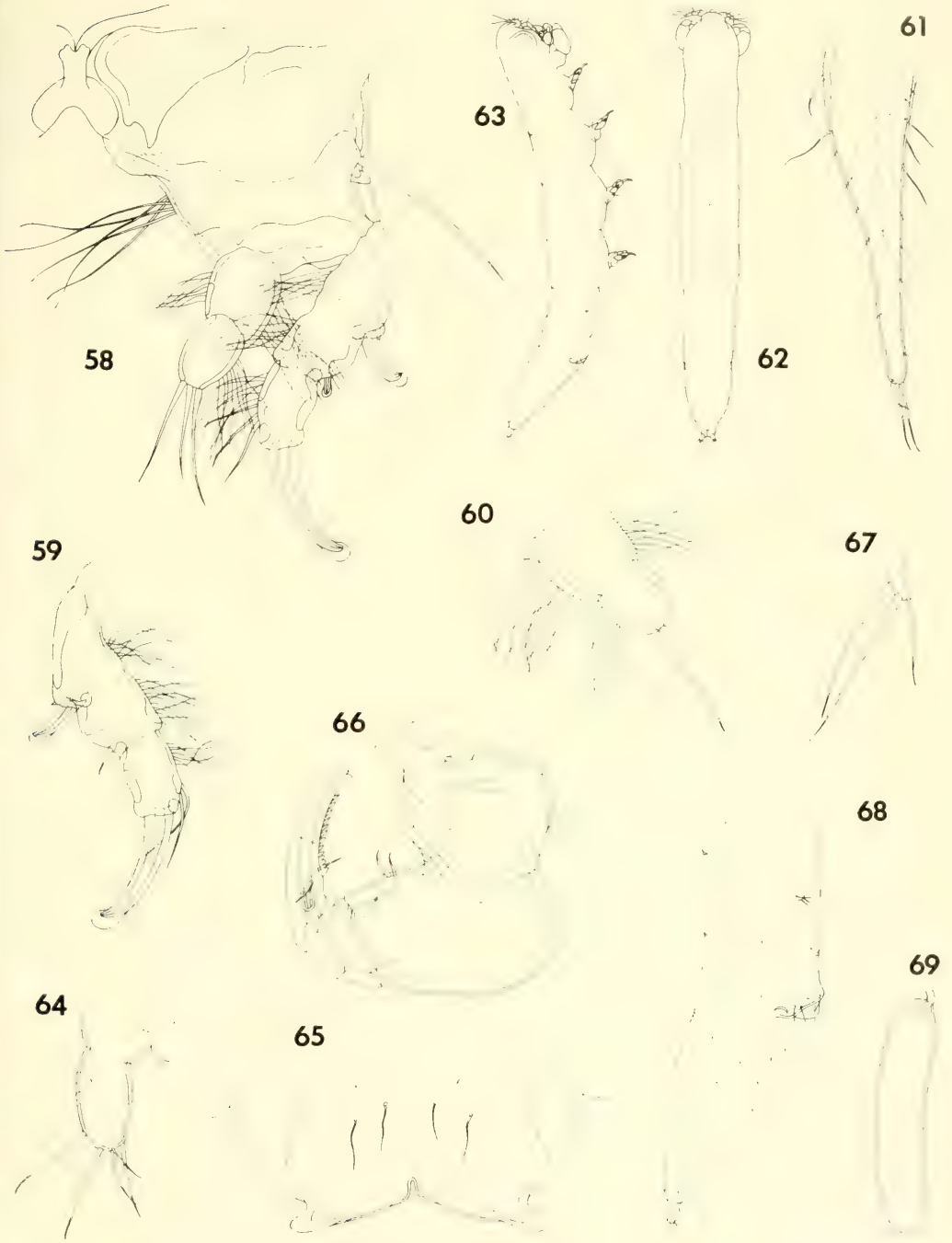


Figures 38–43. *Xarifia exigua* n. sp., male. 38, body, dorsal (B); 39, body, lateral (B); 40, caudal ramus, dorsal (E); 41, maxilliped, inner (E); 42, leg 5, lateral (E); 43, urosome, ventral (H).

Figures 44–47. *Xarifia decorata* n. sp., female. 44, body, dorsal (A); 45, body, lateral (A); 46, urosome, lateral (B); 47, caudal ramus, dorsal (G).

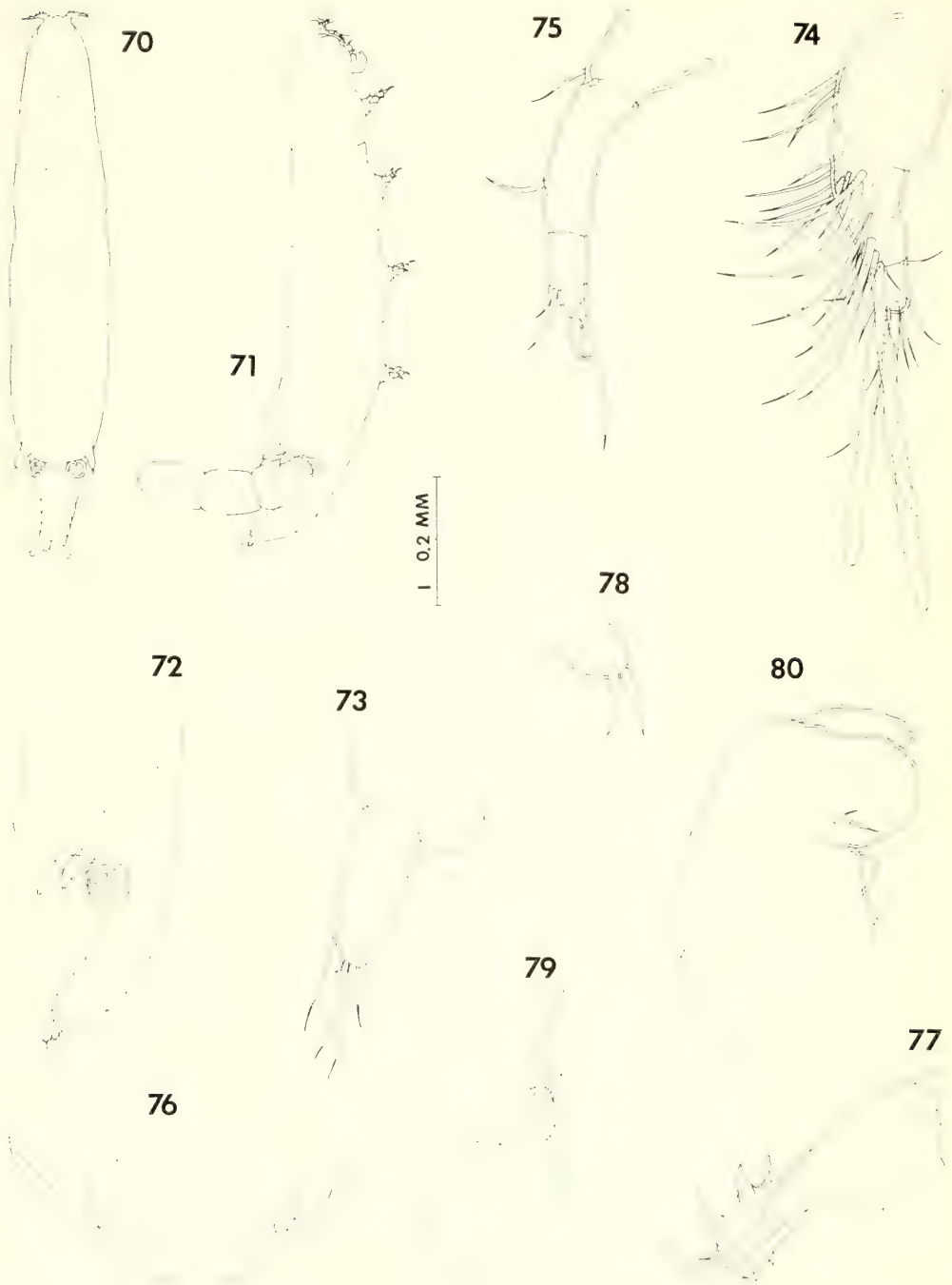


Figures 48–57. *Xarifia decorata* n. sp., female (continued). 48, rostral area, anteroventral (D); 49, anterior end of body, dorsal (F); 50, first antenna, ventral (D); 51, second antenna, ventral (D); 52, labrum, ventral (D); 53, mandible, ventral (E); 54, first maxilla, ventral (E); 55, second maxilla, ventral (D); 56, maxilliped, inner (D); 57, anterior part of body, lateral (F).

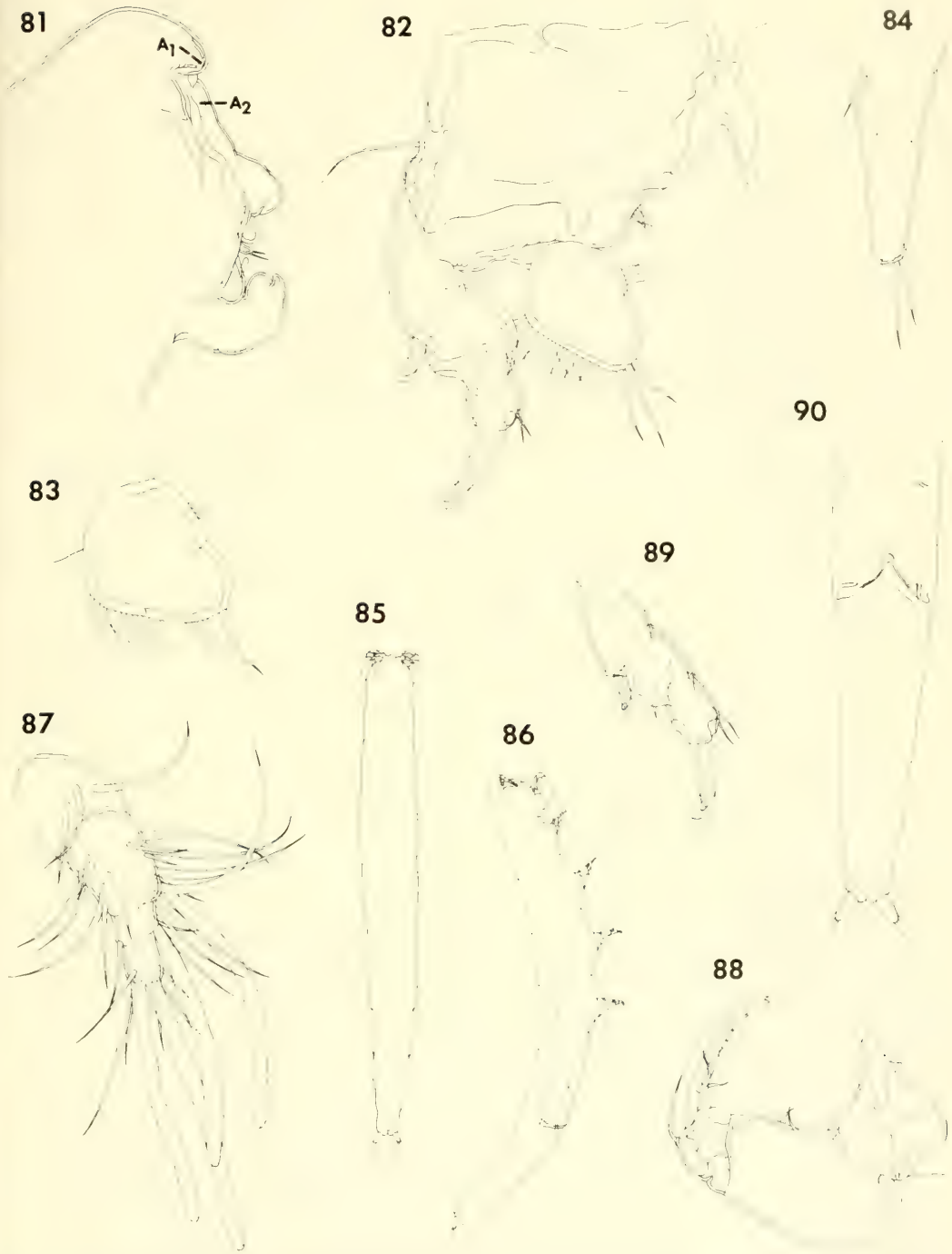


Figures 58–61. *Xarifia decorata* n. sp., female (continued). 58, leg 1 and intercoxal plate, posterior (D); 59, exopod of leg 2, posterior (D); 60, endopod of leg 3, posterior (D); 61, leg 5, lateral (F).

Figures 62–69. *Xarifia decorata* n. sp., male. 62, body, dorsal (A); 63, body, lateral (A); 64, caudal ramus, ventral (C); 65, labrum, ventral (D); 66, maxilliped, inner (G); 67, leg 5, lateral (D); 68, urosome, lateral (B); 69, spermatophore, attached to female, lateral (B).



Figures 70–80. *Xarifia lissa* n sp., female. 70, body, dorsal (A); 71, body, lateral (A); 72, urosome, lateral (I); 73, caudal ramus, ventral (C); 74, first antenna, dorsal (D); 75, second antenna, ventral (D); 76, labrum, ventral (D); 77, mandible, ventral (E); 78, first maxilla, ventral (E); 79, second maxilla, ventral (E); 80, maxilliped, inner (D).



Figures 81–84. *Xarifia lissa* n. sp., female (continued). 81, anterior part of body, lateral (F); 82, leg 1 and intercoxal plate, posterior (D); 83, endopod of leg 3, posterior (D); 84, leg 5, lateral (G).

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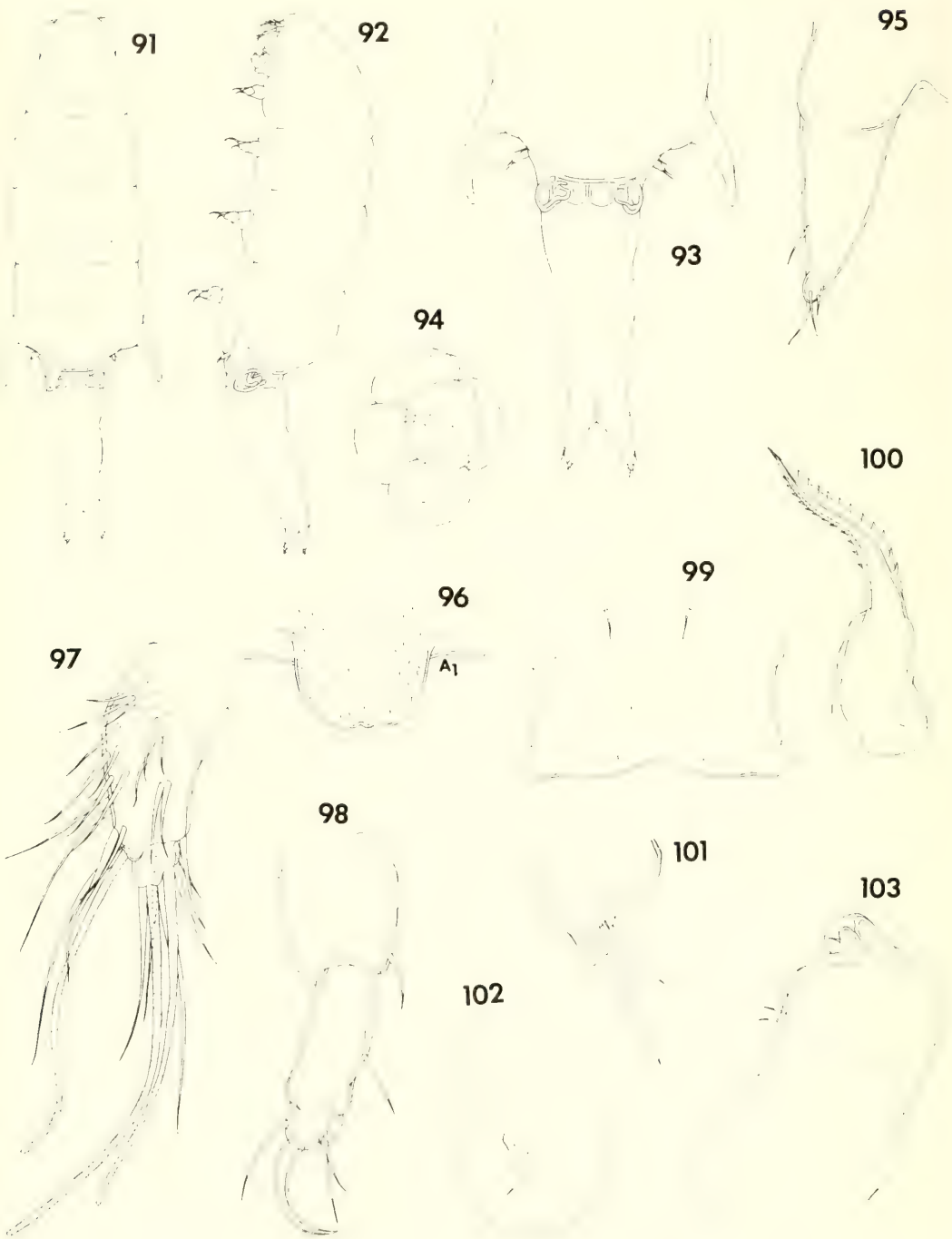
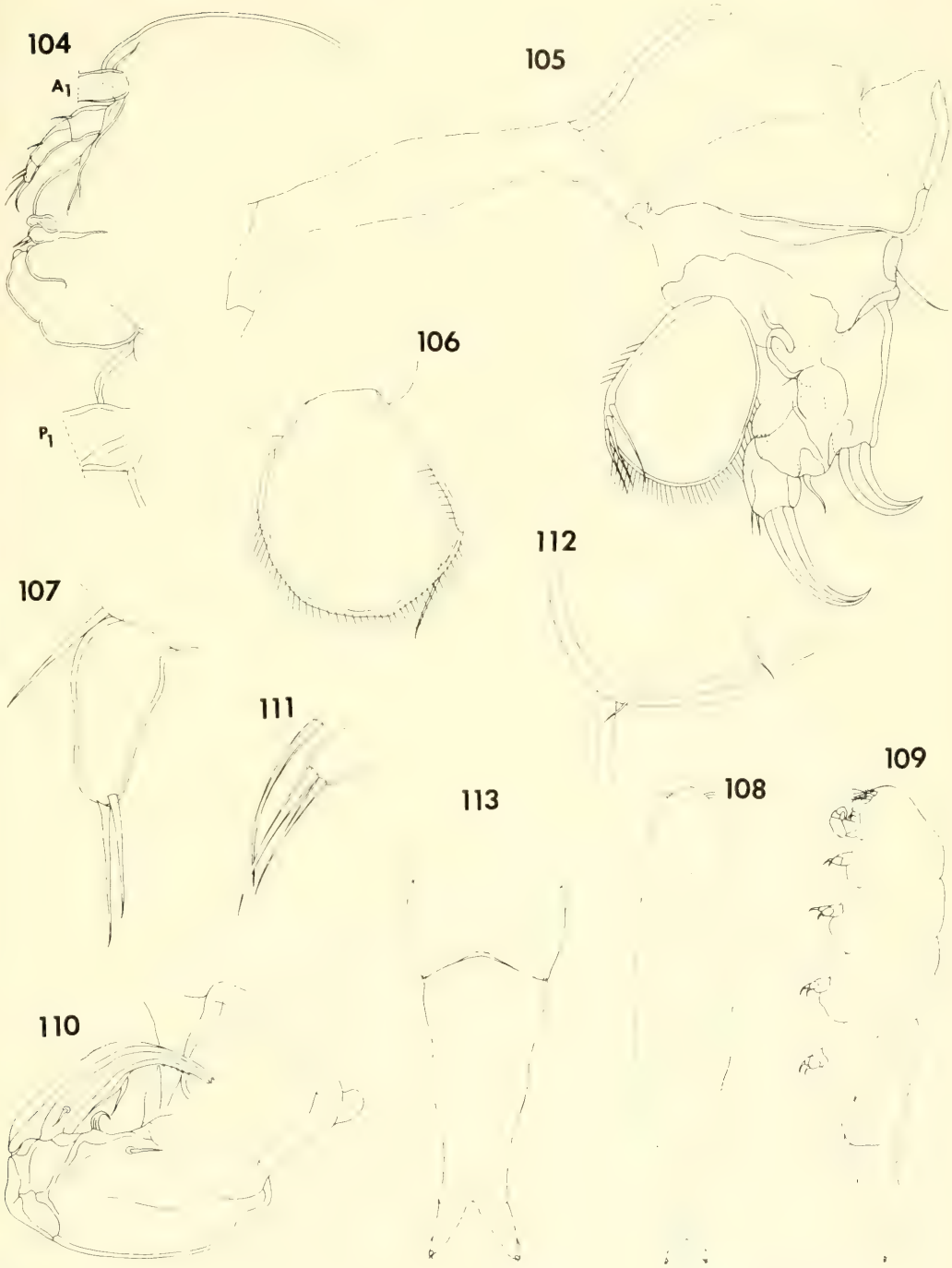


Figures 91–103. *Xarifia obesa* n. sp., female. 91, body, dorsal (A); 92, body, lateral (A); 93, urosome, dorsal (I); 94, egg sac, dorsal (I); 95, caudal ramus, dorsal (G); 96, rostrum, anteroventral (C); 97, first antenna, anterior (D); 98, second antenna, anteroventral (D); 99, labrum, ventral (C); 100, mandible, ventral (E); 101, first maxilla, ventral (E); 102, second maxilla, ventral (E); 103, maxilliped, outer (D).



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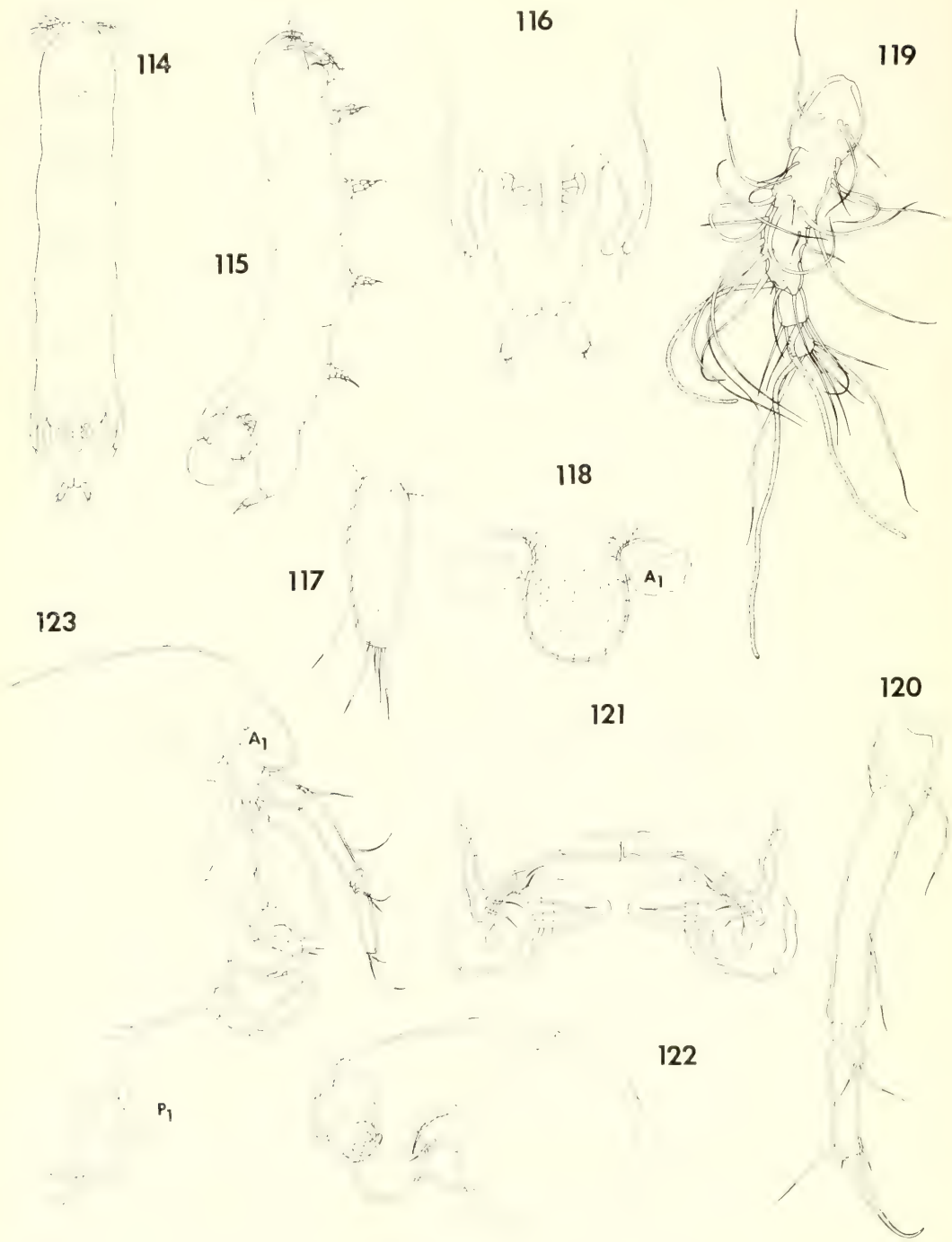
Figures 108–113. *Xarifia obesa* n. sp., male. 108, body, dorsal (A); 109, body, lateral (A); 110, maxilliped, inner (C); 111, leg 5, ventral (E); 112, leg 6, ventral (E); 113, urosome, ventral (B).



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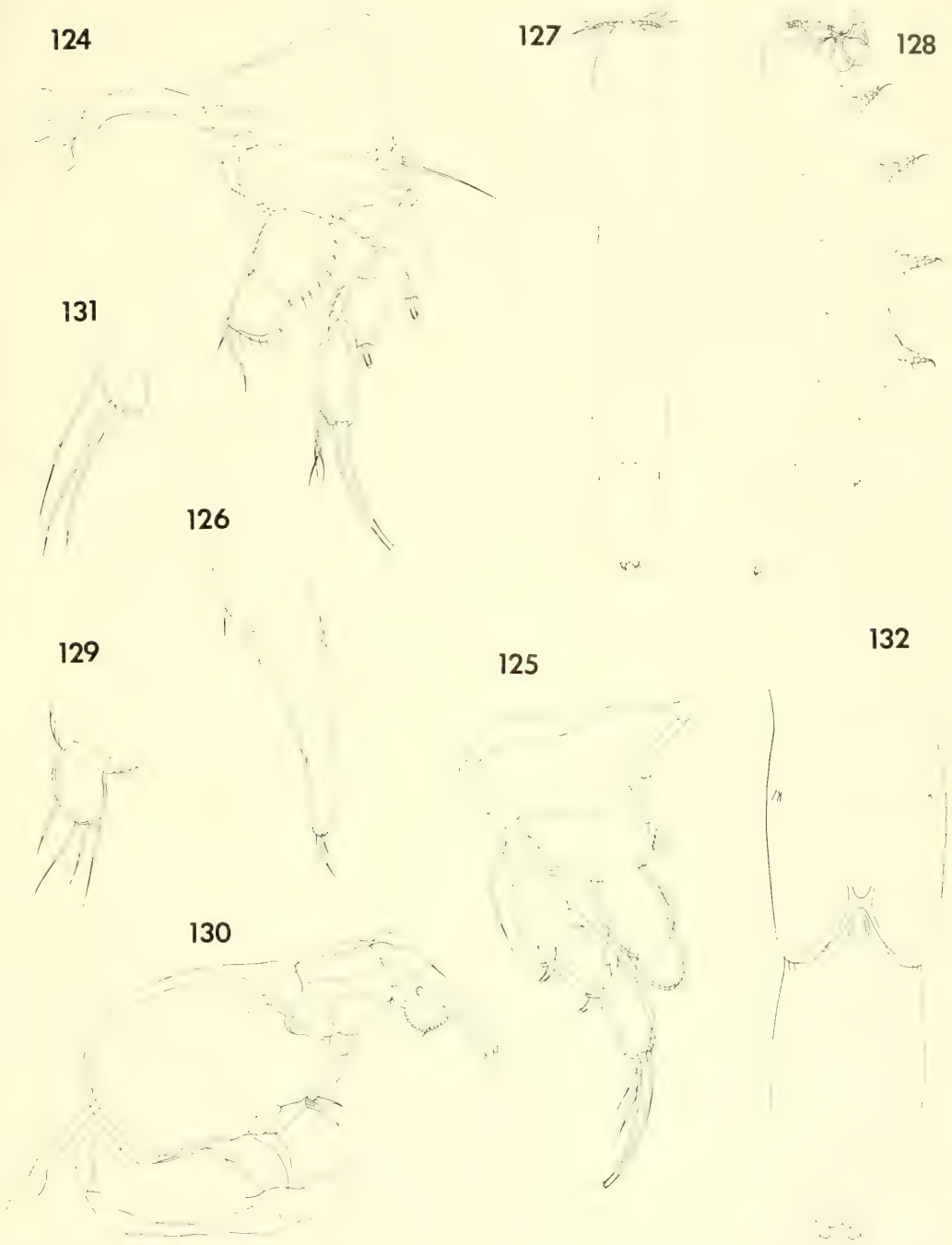

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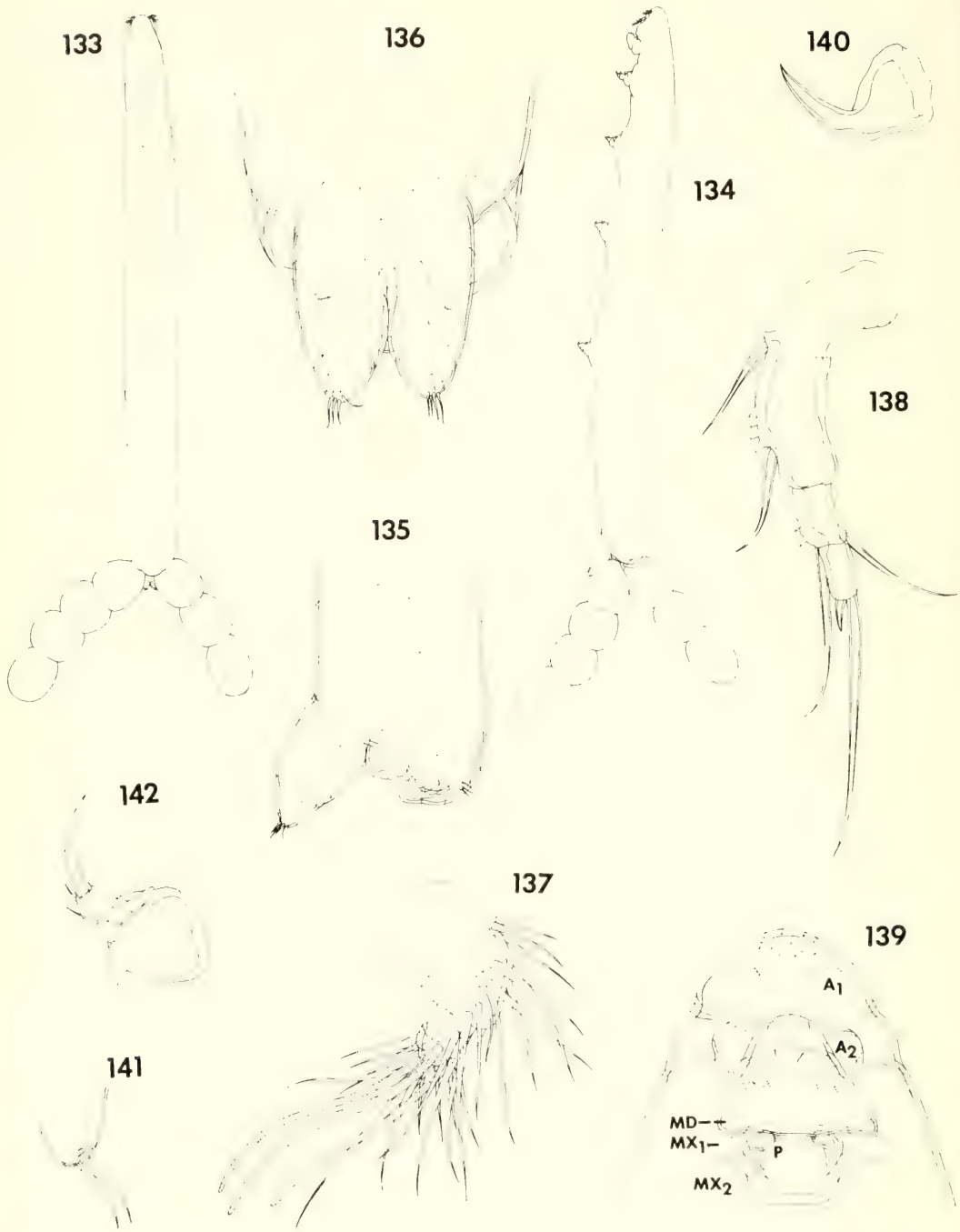

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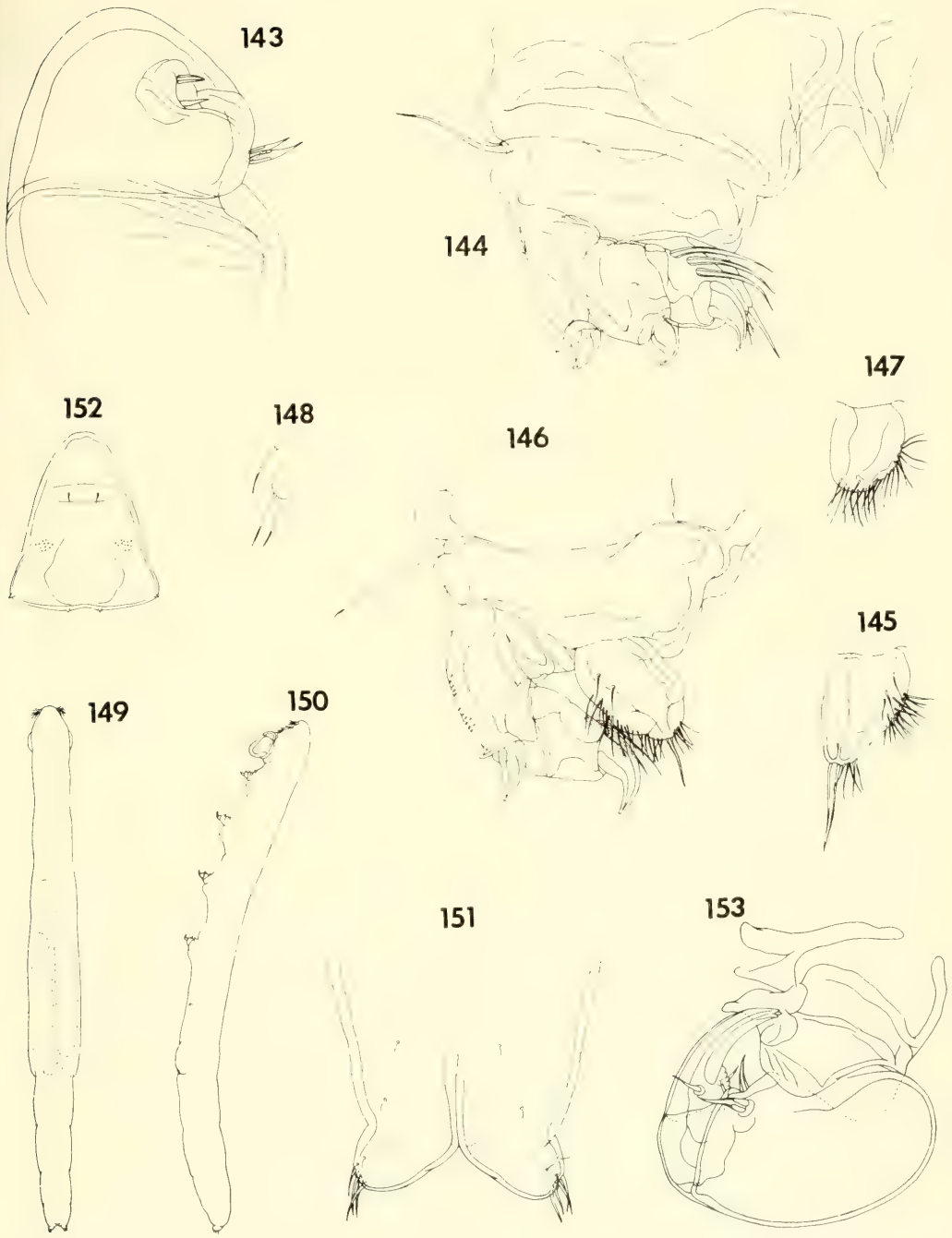

Figures 143–148. *Xarifia temnura* n. sp., female (continued). 143, maxilliped, inner (E); 144, leg 1 and intercoxal plate, posterior (E); 145, endopod of leg 1, anterior (E); 146, leg 2, anterior (E); 147, endopod of leg 3, anterior (E); 148, leg 5, lateral (D).

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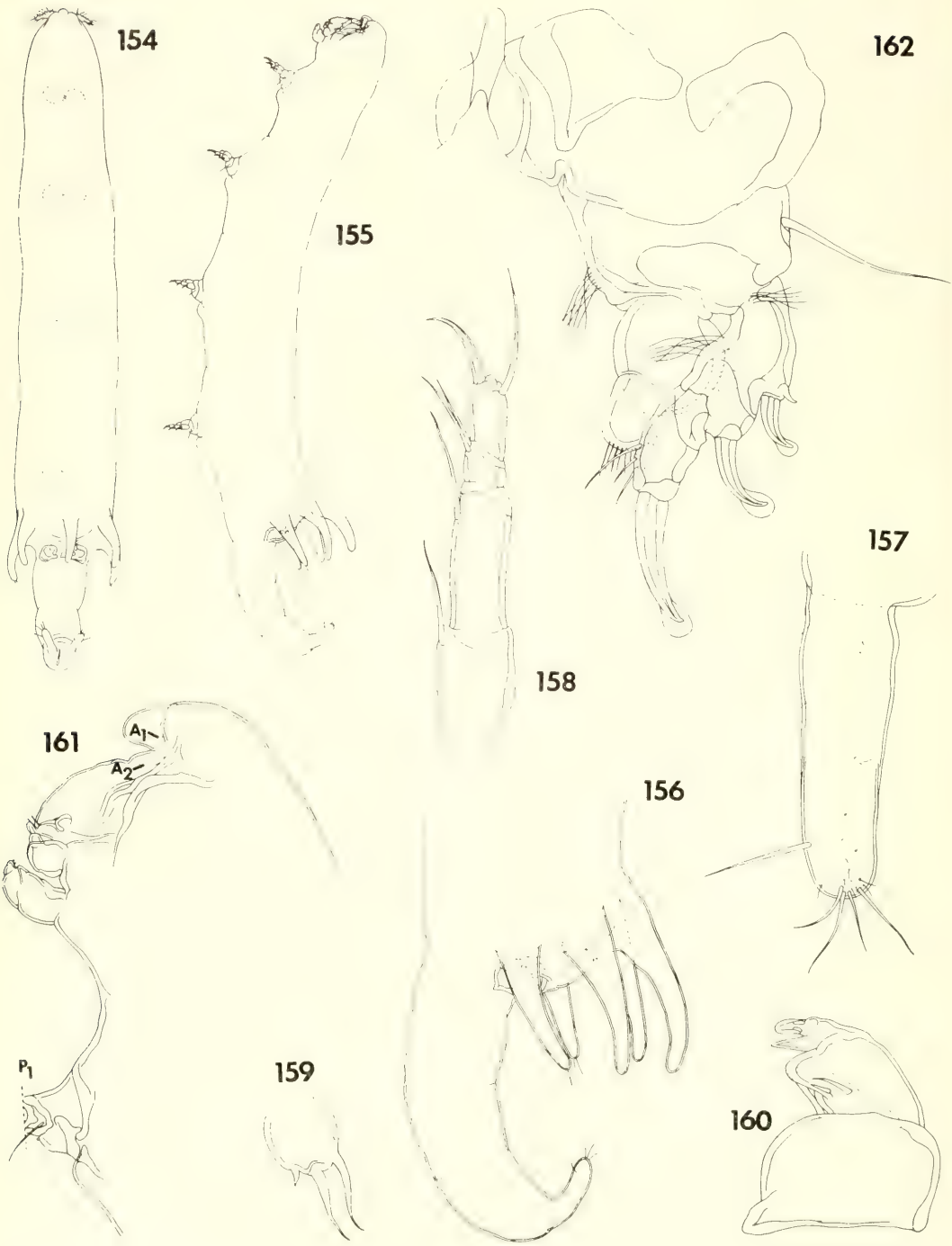

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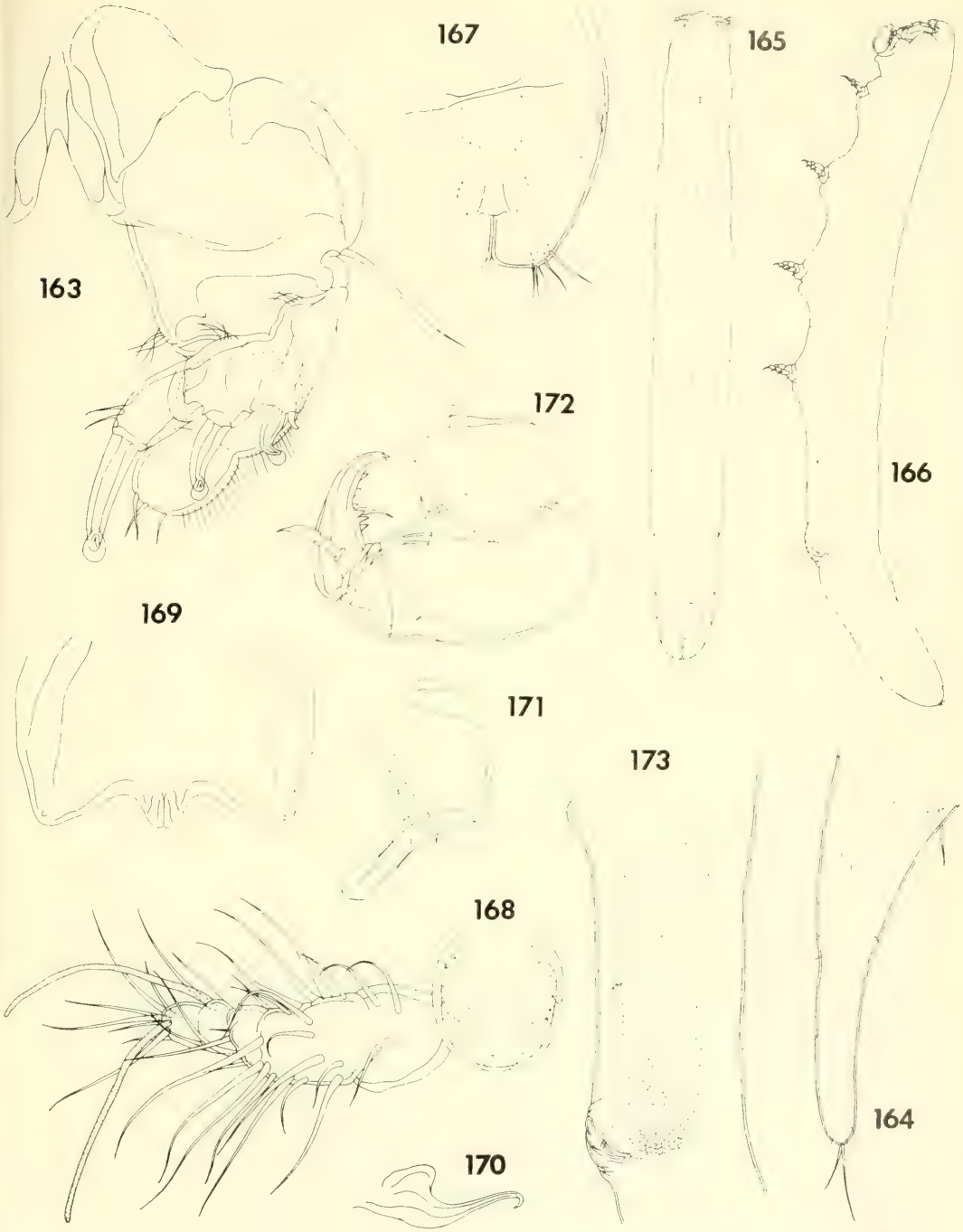
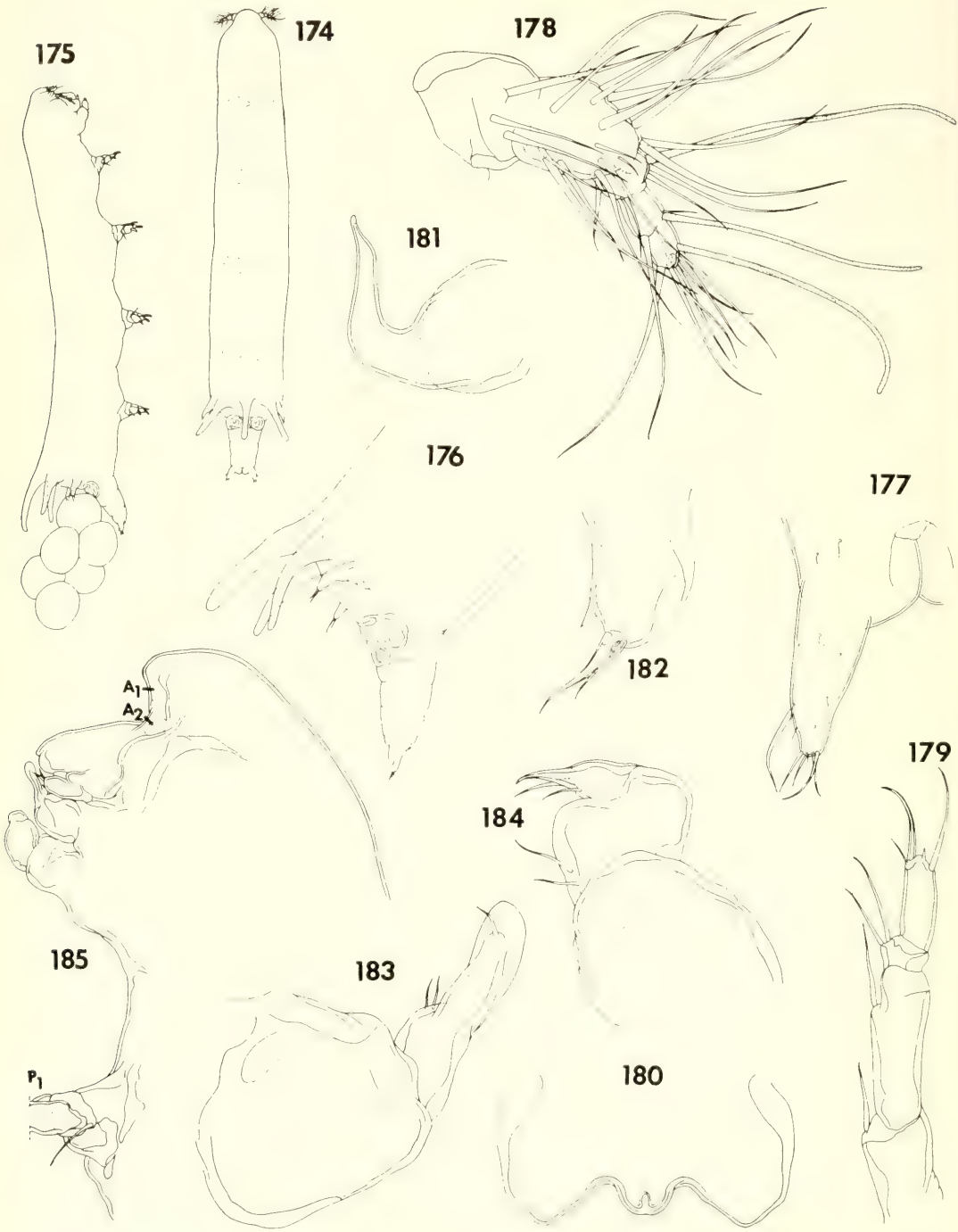
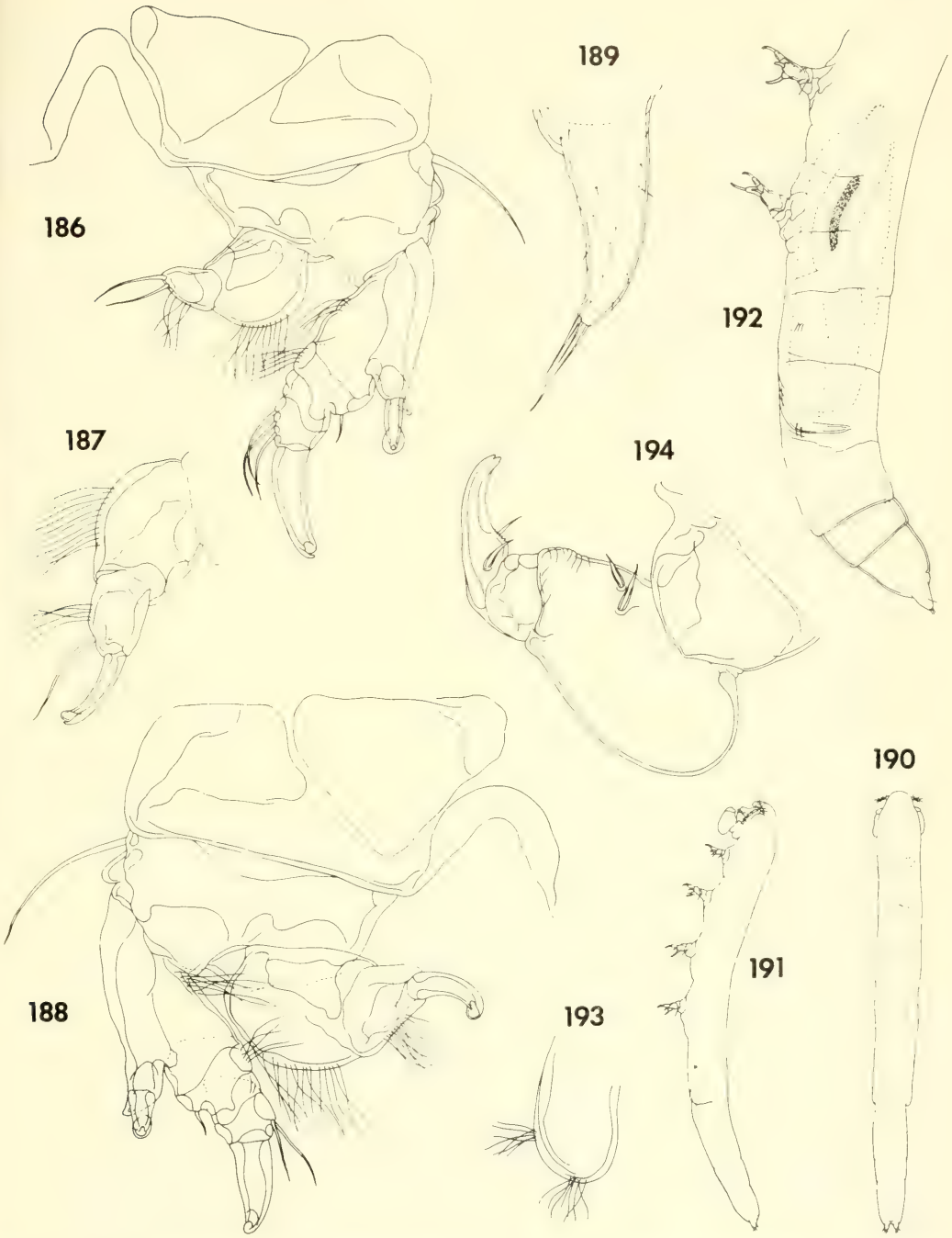


Figures 163–164. *Xarifia anomala* n. sp., female (continued). 163, leg 2 and intercoxal plate, posterior (E); 164, leg 5, lateral (C).

Figures 165–173. *Xarifia anomala* n. sp., male. 165, body, dorsal (I); 166, body, lateral (I); 167, caudal ramus, dorsal (C); 168, rostrum and first antenna, ventral (E); 169, labrum, ventral (E); 170, mandible, ventral (E); 171, second maxilla, anteroexternal (E); 172, maxilliped, medial (D); 173, portion of urosome showing leg 5, leg 6, and position of spermatophore, lateral (H).



Figures 174–185. *Xarifia hamata* n. sp., female. 174, body, dorsal (A); 175, body, lateral (A); 176, urosome, lateral (B); 177, caudal ramus, dorsal (C); 178, first antenna, anterodorsal (D); 179, second antenna, ventral (D); 180, labrum, ventral (D); 181, mandible, ventral (E); 182, first maxilla, posterior (E); 183, second maxilla, posterior (E); 184, maxilliped, posterointernal (D); 185, anterior part of body, lateral (F).



Figures 186–189. *Xarifia hamata* n. sp., female (continued). 186, leg 1 and intercoxal plate, posterior (D); 187, endopod of leg 2, posterior (D); 188, leg 3 and intercoxal plate, posterior (D); 189, leg 5, lateral (C).

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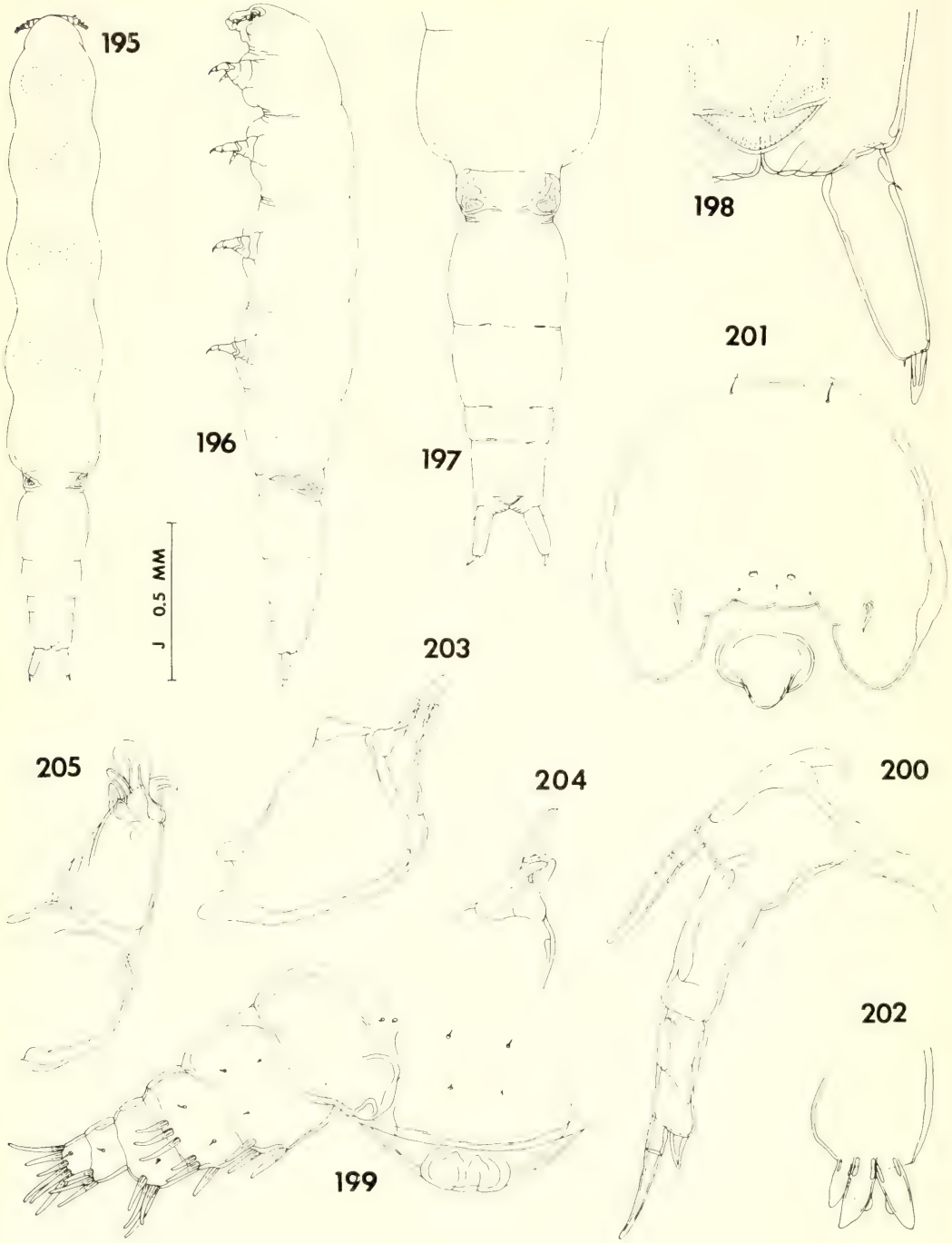
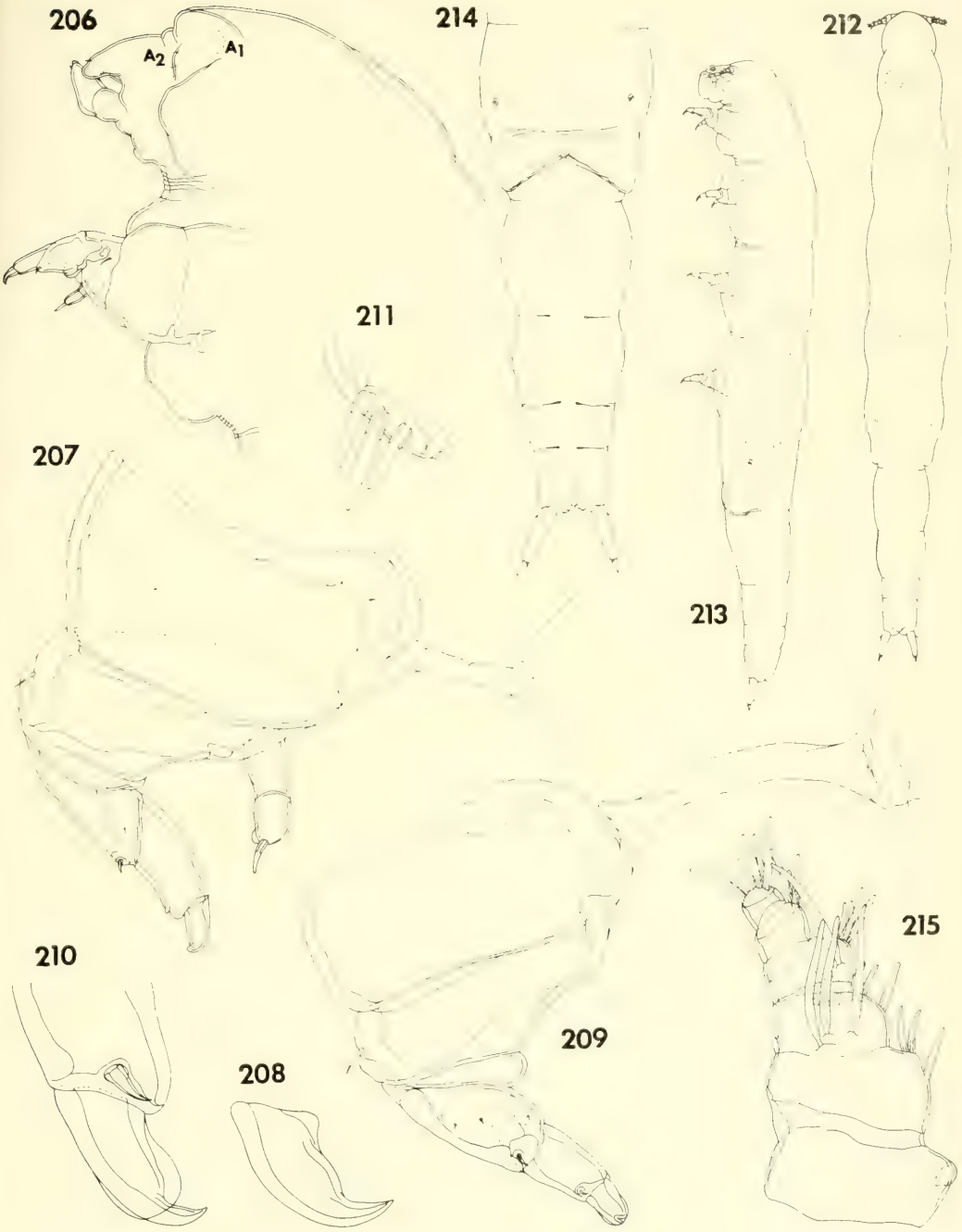


Figures 195–205. *Orstomella faviae* n. gen., n. sp., female. 195, body, dorsal (J); 196, body, lateral (J); 197, urosome, dorsal (I); 198, caudal ramus, dorsal (G); 199, rostral area and first antenna, anterior (C); 200, second antenna, outer (E); 201, labrum and median prominence behind second maxillae, anteroventral (D); 202, first maxilla, anteroventral (E); 203, second maxilla, anteroventral (E); 204, terminal portion of second maxilla, posterior (E); 205, maxilliped, anteroventral (D).



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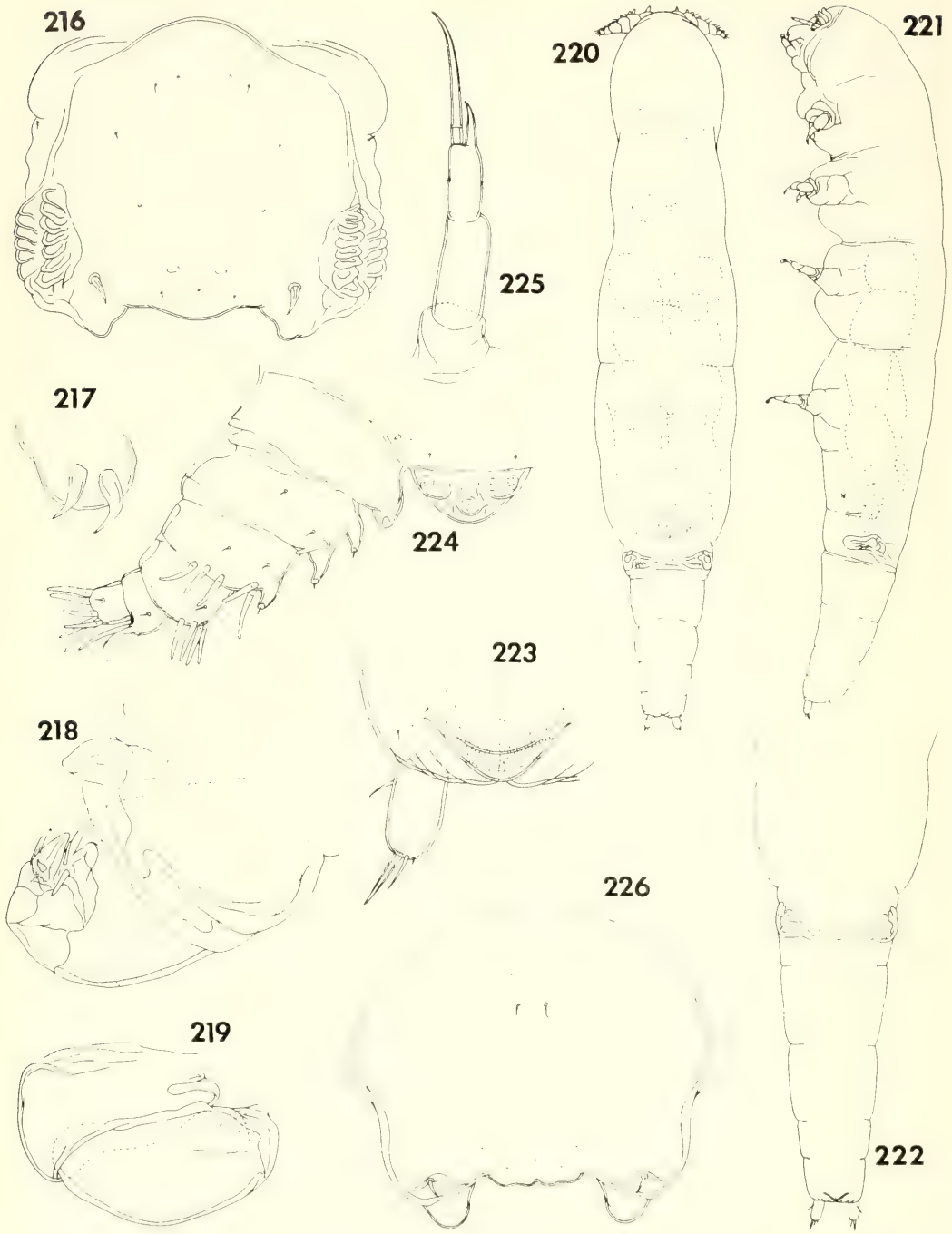
Figures 212–215. *Orstomella faviae* n. gen., n. sp., male. 212, body, dorsal (J); 213, body, lateral (J); 214, urosome, ventral (I); 215, first antenna, posterior (C).



Figures 216–219. *Orstomella faviae* n. gen., n. sp., male (continued). 216, labrum, anteroventral (D); 217, first maxilla, anteroventral (E); 218, maxilliped, anterointernal (C); 219, maxilliped, outer (G).
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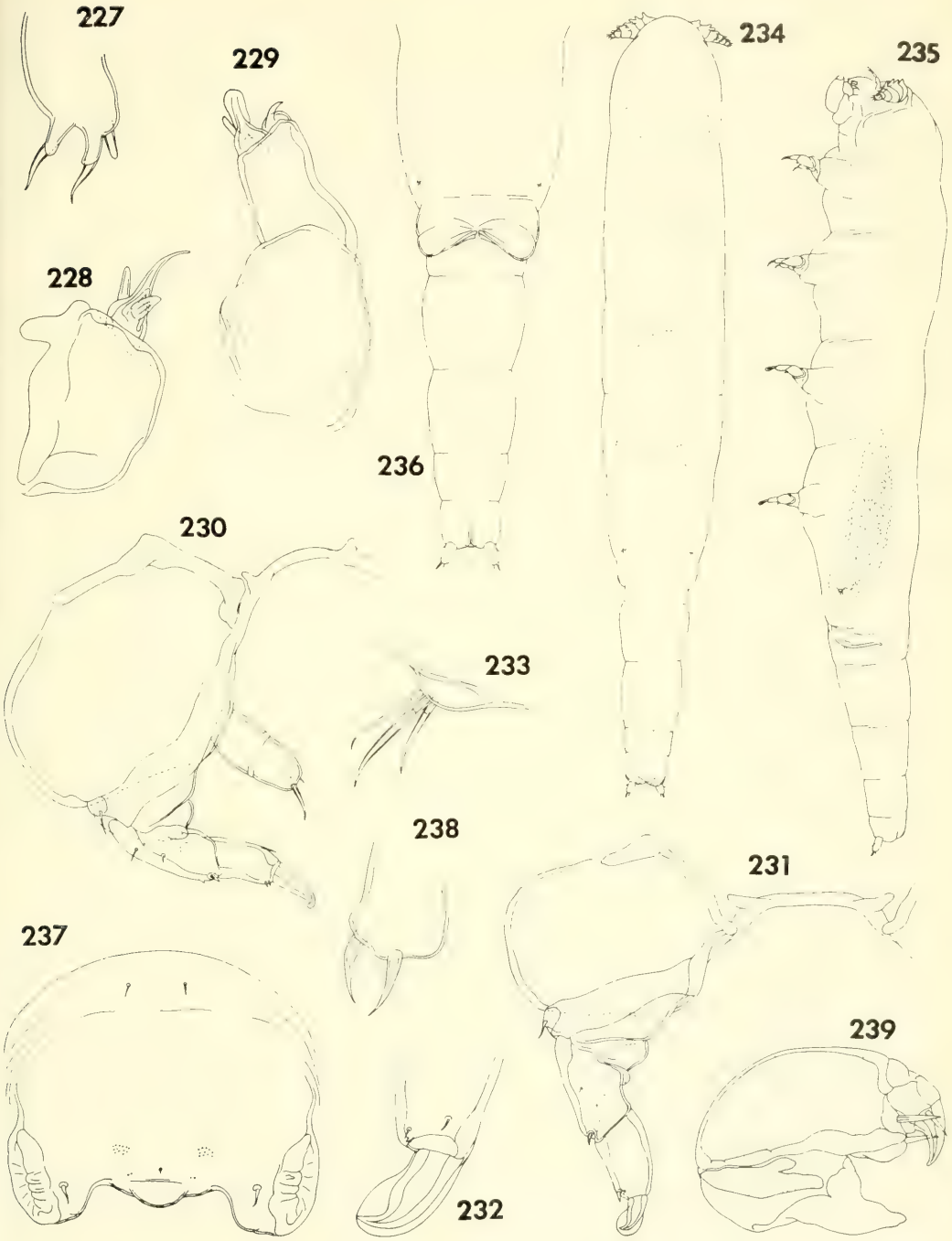

Figures 227–233. *Orstomella lobophylliae* n. gen., n. sp., female (continued). 227, first maxilla, ventrointernal (E); 228, second maxilla, ventrointernal (E); 229, maxilliped, outer (D); 230, leg 1 and intercoxal plate, posterior (C); 231, leg 3 and intercoxal plate, posterior (C); 232, terminal portion of exopod of leg 4, lateral (E); 233, leg 5, ventral (E). Figures 234–239. *Orstomella lobophylliae* n. gen., n. sp., male. 234, body, dorsal (I); 235, body, lateral (I); 236, urosome, ventral (B); 237, labrum, anteroventral (D); 238, first maxilla, outer (E); 239, maxilliped, inner (C).

Bulletin OF THE
Museum of
Comparative
Zoology

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R. F. LAURENT

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 12
MAY 29, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

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Publications Office
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A RE-EXAMINATION OF THE SNAKE GENUS *LYCOPHIDION* DUMÉRIL AND BIBRON

R. F. LAURENT[1]

INTRODUCTION

The last attempt at a comprehensive treatment of the genus *Lycophidion* was provided by H. W. Parker in the form of a key (1933). Later, Parker (1936) added a previously overlooked species. Since then, little progress has been made. A. Loveridge (1936–1942) tried to improve the situation by trinomials that were intended to express the geographical variation of *Lycophidion capense*, which was regarded as a common and almost panethiopian species. This use of trinomials, however, has gone too far, as has already been proved in many other instances: some apparent allopatric patterns were the result of insufficient data, and, even when allopatry is real, the sharpness of the differences and the absence of any hybrid or clinal zones disclose that the specific level has actually been reached. The sympatry of *Lycophidion ornatum* with *L. capense jacksoni* in the African Great Lakes region shows conclusively that *L. ornatum* is not a race of *L. capense*, but a good species (Laurent, 1956). I here provide a restudy of the genus.

The material preserved in the important African collections in the United States has been examined with the hope of a better understanding of the genus.

[1] Instituto Miguel Lillo, Miguel Lillo 205, Tucumán, Argentina.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge that this work has been supported by grant No. GB 1342 from the National Science Foundation. The data were gathered during my stay at the Museum of Comparative Zoology, and on a trip made in 1962 to the Field Museum of Natural History, the United States National Museum, and the American Museum of Natural History. Therefore, my thanks are due to several colleagues and friends who generously put the collections in their custody at my disposal: Dr. D. Cochran (USNM), Mr. C. M. Bogert and Mrs. M. Bullitt (AMNH), Dr. E. E. Williams (MCZ), Dr. R. F. Inger and H. Marx (FMNH).

CHARACTERS UTILIZED

1) *Number of scale rows around the body.* This character has been checked at the three customary levels: the neck, where it has some variability, mid-body, where it is quite constant, and the vent level, where it shows little variation. The species examined here all have 17 mid-body scale rows; the posterior counts are generally 15, except for *irroratum, ornatum* and *uzungwense*.

2) *Ventrals.* The number of ventrals, the individual variation of which has been greatly overestimated by previous authors, is the best clue to heterogeneity in any population sample, as can be seen in the

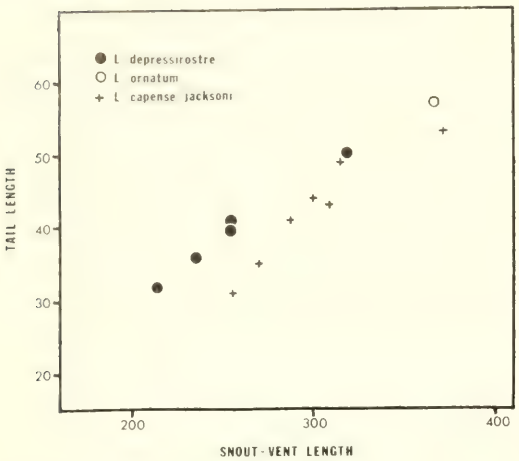

Figure 1. Tail length in relation to snout-vent length in some males of *Lycophidion* from Sudan.

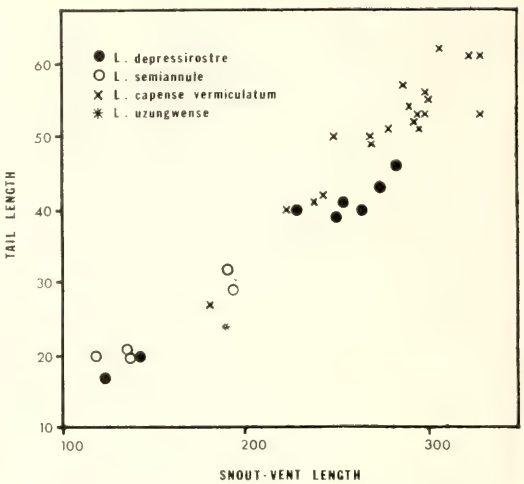

Figure 2. Tail length in relation to snout-vent length in males of *Lycophidion* from southeastern Tanzania.

tables as well as in the section dealing with the non-dimensional species.

3) *Subcaudals.* The number of subcaudals is nearly as useful as the number of ventrals, but it must be remembered that the tail is sometimes mutilated and that the count can therefore be misleading if the injury has not been recognized.

4) *Apical pits.* The number of apical pits is a very good character which, however, has the drawback of often being difficult to ascertain or even not determinable on poorly preserved individuals.

5) *Contact between the postnasal and the first labial.* This is a good character rightly emphasized by H. W. Parker when he described *L. ornatum.* It is also present in the western species *semicinctum* and *irroratum.*

6) *Relative length of the tail.* There are some obvious differences in this respect between species and subspecies (cf. scatter diagrams, Figs. 1, 2, 3, 4).

7) *Ratio of the eye diameter to the distance of the eye from the lip.* This ratio, usually used in keys, is a poor character because of the negatively allometric growth of the eye and much intrinsic variability. Some species have definitely larger eyes than others, but this character can hardly be relied upon for identification (cf. Fig. 11).

8) *Length versus width of the frontal plate.* Although this ratio is part of routine descriptions, it is not useful in the genus *Lycophidion.*

9) *Length of the parietals versus length of the snout.* This character, used by Parker (1933) for distinguishing *semicinctum* from other forms, is indeed excellent and is not disturbed by allometry: all other forms differ from *semicinctum* in this feature.

10) *Color pattern of the dorsal scales.* It has been recognized here that two basic patterns are in existence and that, being correlated with other differences, they are taxonomically significant: each dorsal scale is generally white bordered, but some populations also have white dots on each scale.

11) *Color pattern of head.* Some conspicuous features like the broad light band surrounding the snout in some species were already well known. But some other aspects of pattern have been overlooked in some populations. For example, the snout band may be very narrow, and sometimes interrupted, while the top plates (frontal, parietals, etc.) may have no markings whatever; in other populations, the top of the head has light dots or a light marbled pattern.

12) *Color of the belly.* In the popula-

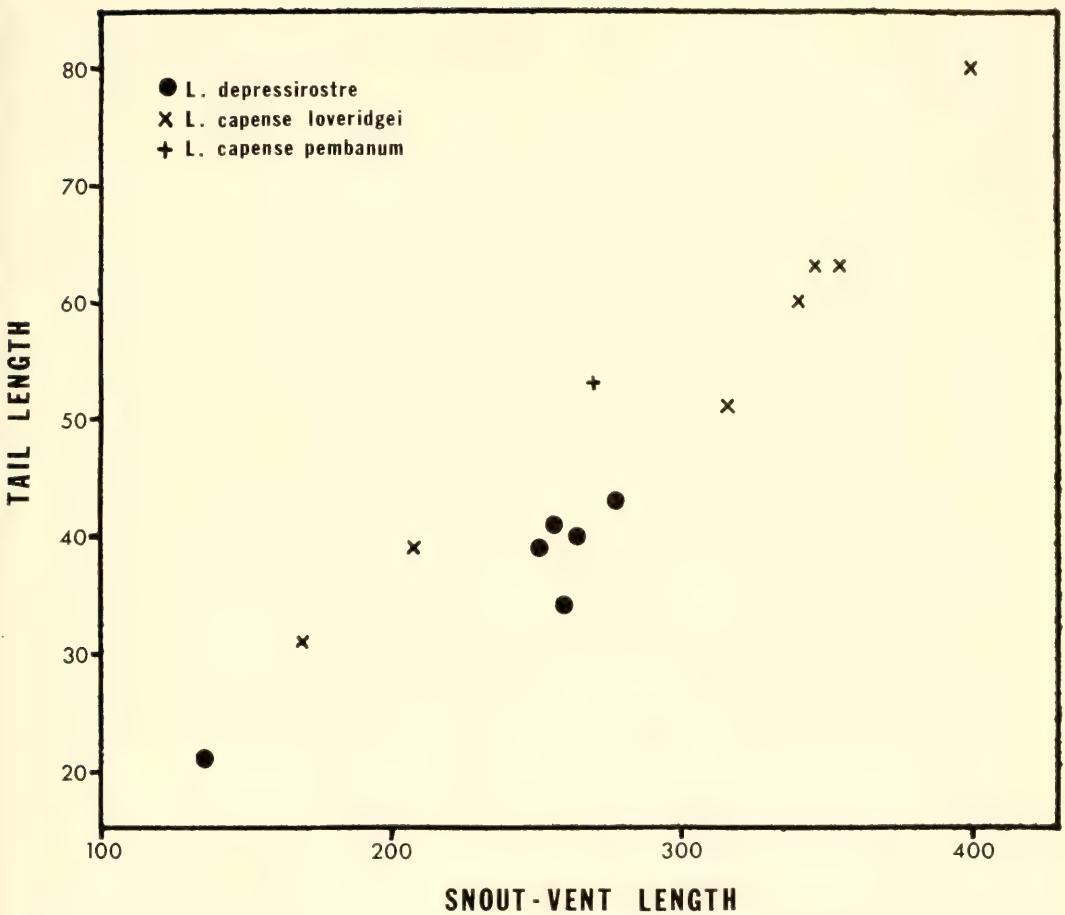

Figure 3. Tail length in relation to snout-vent length in males of *Lycophidion* from coastal East Africa.

tions from South Africa, the belly is light; in the others it is dark.

13) *Color of the throat.* This is light, with or without dark spots, in some forms; dark, with or without light markings, in others.

Such other characters as labials, oculars, and temporals do not appear to have any taxonomically significant variation in this group.

RECOGNITION OF NON-DIMENSIONAL SPECIES

The Region of the Great Lakes

The sympatry of two species—*L. capense jacksoni* Boulenger and *L. ornatum* Parker—in the Great Lakes region has been abundantly documented by Laurent (1956, 1960).

Western Africa

It has long been recognized that three species live side by side in western Africa: *L. laterale* Hallowell, *L. irroratum* Leach, *L. semicinctum* Duméril and Bibron. *L. capense* has also been cited by many authors as occurring there. In addition, some specimens from this region in the Museum of Comparative Zoology have been identified as *L. ornatum.* In reality, setting

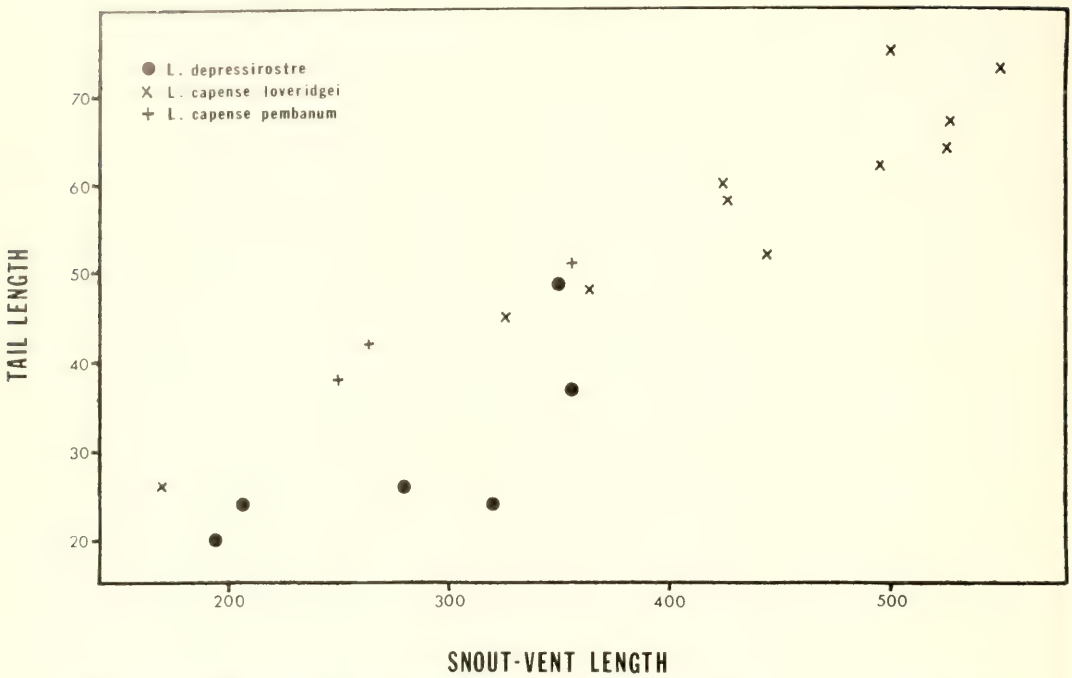

Figure 4. Tail length in relation to snout-vent length in females of *Lycophidion* from coastal East Africa.

aside *L. laterale*, which is easily identified, only two species are present in the collections that I have examined: *irroratum* and *semicinctum*. Since so many specimens have been misidentified as *capense* or *ornatum*, I believe, until proof of the opposite, that all such records are founded on similar misidentifications and that these species are actually absent from *western* Africa.

The obvious differences between the two western species are as follows.

		irroratum	*semicinctum*
Apical pits		2	1
Ventrals	♂♂	165–182	183–193
	♀♀	169–184	196–211
Subcaudals	♂♂	37–44	47–58
	♀♀	no difference	

Sudan

The available Sudanese material can be split into three groups.

		A	B	C
Ventrals	♂♂	182–195	163–171	206
	♀♀	188–202	167–178	
Subcaudals	♂♂	34–42	34–39	47
	♀♀	29–33	26–28	
Length of the tail in percentage of the total length (Fig. 1)	♂♂	10.8–13.5 (generally less than 13%)	13–13.9 (at least 13%)	14.9
	♀♀	8.3–9.9	8.5–10.2 (no difference)	

Labials in contact with the postnasal	1–2	1–2 (only in one specimen)	2
Dorsal scale rows	17–17–15	17–17–15	17–17–17
Color of the dorsal scales	brown with a broad light border at the apex but without white dots	brown with or without a narrow light border and generally with white dots near the apex	like B
Color patterns of head	light markings limited to the rostral, the nasals, anterior labials and sometimes a narrow line around the snout	light markings: a large white zone covering not only the rostral and the anterior labials but also invading almost completely the loreal and partly the internasals, prefrontals, preoculars and the borders of postoculars (Fig. 9)	like B, but a still larger white snout band
Size of the eye	small	larger	still larger

The forms A and C are not separable from the two species which are also sympatric in the Great Lakes region—namely, *L. capense jacksoni* and *L. ornatum*—but the form B does not appear to have been described. A and B have been merged under the name of *Lycophidion capense capense* by Loveridge, 1957.

Southeastern Tanzania

Again three distinct species are sympatric in the Liwale region.

		D	E	F
Ventrals	♂♂	182–195	155–165	148
	♀♀	192–203	161–174	
Subcaudals	♂♂	43–52	34–36	31
	♀♀	33–41	22–31	
Relative length of the tail in percentage of the body length	♂♂	generally more than 16.5%	generally less than 16⅔%	less than 16⅔% (Fig. 2)
	♀♀		no significant difference	
Dorsal scales		brown with a light border but no light dots	a light border *and* white dots	a light border, no light dots
Head		generally light dots or vermiculations all over the head	generally no light dots or vermiculations but some plates are light bordered, especially between the eye and the nostril	no light dots but a white band surrounding the snout
Throat		generally light with dark markings	rather dark with light markings	uniform greyish
Eye		large (negative allometry)	smaller (growth seems isometric)	smaller (Fig. 3)

Loveridge has cited D as *L. capense capense* and E as "intermediates between *capense* and *acutirostre*." F is a specimen of *L. semiannule* in the Field Museum of Natural History.

Coastal Kenya and Tanzania plus Usambara and Uluguru Mountains

Although there is not here a single case of precise sympatry in the narrowest sense of the term (*i.e.* no locality from which we see specimens of two species), the distributions of two very distinct species are so interdigitated that there is little doubt that the fact reflects some ecological segregation.

		G	H
Ventrals	♂ ♂	195–211	155–165
	♀ ♀	205–219	167–176
Subcaudals	♂ ♂	47–58	31–37
	♀ ♀	40–44	23–29
Length of the tail in percentage of the snout-vent length	♂ ♂	generally $> 16.5\%$ (except one individual out of six: 16.2%)	$< 16.5\%$
	♀ ♀	$> 12\%$	$< 12\%$ (except 1 out of 6: 14%)
Eye		larger (diameter $> 170\%$ of the distance between the eye and the lip, in 11 specimens out of 16, the exception being among the larger individuals)	smaller (diameter $< 170\%$ of the distance between the eye and the lip in 9 specimens out of 13, the exception being among the smallest individuals)
Dorsal scales		a light border, no light dots	a light border and light dots
Head plates		with light dots or vermiculations	generally without white dots on the top of the head except in specimens from Kenya; rostral and nasal light colored; sometimes a white band around the snout
Throat		light	dark

Again Loveridge has cited one form as *L. capense capense*, the other as "intermediates between *capense* and *acutirostre*."

Somali Region

I have already (1956) stressed the improbability that Parker's material (Parker, 1949) of *Lycophidion capense* would really involve only one species, since the range of variation for ventrals is unusually wide. However, there is no gap in this variation large enough to prove unequivocally the coexistence of two sympatric species. With the hope of finding other distinguishing characters, I asked for the loan of material from Miss A. G. C. Grandison of the British Museum who sent it with her customary kindness. The differences are admittedly not so clear cut as those which are obvious in other regions (Sudan or East Africa), but in my opinion they are sufficient to strongly suggest the existence of two sympatric sibling species.

		I	J
Ventrals	♂ ♂	174–166	157
	♀ ♀	181–180	165, 170
Subcaudals	♂ ♂	35–34	33
	♀ ♀	30–32	26, 27
Dorsal scales		one or several subapical white spots	no white subapical spots, a light border in one specimen

Head	lateral white markings narrow, sometimes with vermiculations or spots on the crown		rostral and nasal light colored with some light dots on the crown; white lateral markings narrow in one specimen

ALLOPATRIC RELATIONSHIPS

1) South African Populations

In South Africa only one species can be recognized. It is, of course, *Lycophidion capense*. What are its relationships with populations from neighboring areas?

		capense from S. Africa	Southwest Africa	*multimaculatum* Rhodesia and Angola	*semiannule* Mozambique
Ventrals	♂♂	180–188	167–177	173–177	134–148
	♀♀	188–190	177–187	172–183	144–146
Subcaudals	♂♂	36–40	31–37	31–42	27–31
	♀♀	30–39(?)	26–30	24–35	25–30
Belly		light	generally light	generally dark	dark

These data suggest that the populations from South Africa, Southwest Africa, Rhodesia and Angola belong to a single species, *Lycophidion capense*, and that *L. semiannule*, with considerably lower ventral counts and also color differences, is indeed another species. The populations from Southwest Africa differ from typical *capense* in lower ventral and subcaudal counts. From *multimaculatum* they differ only in the lighter belly, and this difference is so likely to be clinal that no racial discrimination appears necessary. Within the *multimaculatum* populations from Rhodesia, the color of the belly, which is dark in northern populations, seems to become lighter in southern populations; this variation is likely to be clinal; the difference in ventral and subcaudal counts is supposed not to be clinal and the validity of the name *multimaculatum* rests on this assumption, which needs confirmation.

In Southwest Africa, Mertens (1955) reported a male *Lycophidion* with 197 ventrals, which is quite outside the range of variation of the *capense* populations from this region. It must belong to another species, and I suggested (Laurent, 1964) that it probably is *L. hellmichi*, a species that I described from Moçamedes, Angola.

2) Central African Populations

The material available for study is inadequate, but previous data (Laurent 1956, 1960) show a definite step-cline in the ventral and subcaudal counts between Fizi and Lubondja, southern Kivu, Congo.

The southern populations belong to the *capense* subspecies *multimaculatum*. The northern populations have been referred to the *capense* subspecies *jacksoni* Boulenger, which appears to have a rather large range extending to Lake Rukwa, to Kilimanjaro, to Ethiopia (syn. *abyssinicum* Boulenger), and to the Sudan (= form A in Sudan population analysis). Indeed, I am unable to find any reason for taxonomic discrimination between the northern and southern Central African populations, which are remarkably alike. The geographic variation within *multimaculatum* is considerable as far as color is concerned, since not only is there a cline in belly color from south to north, but the light punctations or vermiculations of the head plates, so conspicuous in Rhodesian samples, disappear in northern populations from Lunda Province in Angola and Katanga. In this regard these northern populations are similar to *jacksoni*, in which light markings of the head are reduced to a narrow line on the sides of the snout or are altogether absent. Here are the squamation differences between *jacksoni* and *multimaculatum*:

	jacksoni (Northeastern Congo, Sudan, Uganda, Rwanda, Burundi, Tanzania)	*multimaculatum* (Southern Congo, Zambia, Angola)
Ventrals	176–192	167–180
	180–202	165–183
Subcaudals	34–45	31–42
	28–38	24–35

3) East African Populations

Three non-dimensional species (species D, E, and F above) are distinct in southeastern Tanzania; two (species G and H above) are distinct in the coastal region adjacent to the East African islands. What are the interrelationships of these five populations?

The third form (F) from southeastern Tanzania is obviously *L. semiannule*, previously recorded only from Mozambique and Zululand. The forms E and H are the same and have been cited as intermediates between *L. capense* and *acutirostre* (Loveridge 1933, 1936b, 1942). The Sudanese populations (B) are hardly different except in their size. They can safely be considered as conspecific, and the different size, owing to a large distributional gap in western Kenya, northwestern Tanzania and Uganda, cannot be treated as a clear-cut justification for even subspecific recognition.

The relationships of E, F and B with allopatric forms have now to be investigated. They have much in common with *semiannule*, as indeed Loveridge (1933) noticed when he considered the samples as "intermediates" between *capense* and *acutirostre*; the latter is a synonym of *semiannule*. However, they are sympatric with *semiannule* in southeastern Tanzania so that, if they perhaps were geographic races in the past, the boundary being the Rovuma River, they are not so now. Another possible subspecific relationship is with western *L. irroratum*, but the distributional and morphological gaps are such that any taxonomic decision in this direction would be gratuitous.

The forms D and G are similar in their coloration: head plates vermiculated, no light dots on the dorsal scales, dark belly but light throat. They are also similar in the relative dimension of the eye and the relative length of the tail. They differ in their ventral and subcaudal counts, and the available data suggest a rather abrupt difference near the Uluguru Mountains rather than a cline. It therefore seems logical to treat D and G as subspecies of one species.

Then, the question arises: Which species? Have these two races other subspecific relationships with other allopatric forms? We reject *L. ornatum*, the main characters of which (snout with light band, postnasal not in contact with the first labial, 17 scale rows in front of the anus) are not shared by D and G. *L. capense jacksoni* occurs not very far from the northern form G in the Kilimanjaro region and also on the shores of Lake Rukwa. (G is also present at the northern tip of Lake Nyasa.) In spite of this proximity, the differences between G and *jacksoni* are very clear cut: G has much higher ventral and subcaudal counts, and a head with light vermiculations. Therefore, although we have no data on the populations from central Tanzania it seems rather doubtful that any genetic continuity exists between these two groups of populations. However, if the head vermiculations are missing in *jacksoni*, they exist in southern populations of *multimaculatum* and in *capense* itself; moreover, the coloration of the individual dorsal scales, generally without light punctation, is almost constantly observed from the Cape to the Sudan; finally, the throat is also generally clear in the same populations.

For these reasons, it seems advisable to treat these two East African forms as races of *L. capense*.

4) The Populations from the East African Islands (Pemba and Zanzibar)

The specimens supposed to come from Zanzibar must be treated with suspicion, especially those in the old collections. It has been repeatedly shown that the origin of specimens alleged to have come from Zanzibar was quite different. This was apparently the case for the cotypes of *L. acutirostre* Günther, presumably collected in Mozambique. A specimen in the MCZ collection (MCZ 5992) poses such a problem. It is a male with 169 ventrals, 42 subcaudals, 17 scale rows in front of the anus, and 2 apical pits. Although the alleged locality is Zanzibar, the specimen is obviously *L. irroratum*. More recently collected specimens from Zanzibar have all the characters of the coastal populations of *L. capense* except that the white dots on the head are rather indistinct.

Specimens from Pemba Island, however, have a very distinct color pattern: the head is light colored with dark spots (Fig. 13), a pattern somewhat recalling that of *Miodon collaris*. This population is obviously worthy of recognition, but can it be included in one of the two species existing in coastal East Africa? It has much more in common with G than with H, but still more with the southeastern Tanzania D, as can be seen on the following chart.

		D	G	H	Pemba
Ventrals	♂ ♂	182–195	195–211	155–165	172
	♀ ♀	192–203	205–219	167–176	179–180
Subcaudals	♂ ♂	43–52	47–58	31–37	46
	♀ ♀	33–41	40–44	23–29	37–40
Relative length of the tail (% of snout-vent length)	♂ ♂	generally > 16.5%	generally > 16.5%	< 16.5%	19.8%
	♀ ♀	generally > 12%	> 12%	< 12%	14.4–16.3%
Dorsal scales		a light border	a light border	white dots	a light border
Head		vermiculations	vermiculations	no vermiculations	light background with dark spots
Throat		light	light	dark	light

Thus, it appears that this new form from Pemba Island is a subspecies of *L. capense*.

SYSTEMATIC ACCOUNT

Lycophidion irroratum (Leach)

Coluber irroratus Leach, 1819, in Bowdich, T. E., Mission from Cape Coast Castle to Ashantee: 494.

Lycophidium irroratum Angel, 1933, Bull. Com. Etud. Hist. Scient. AOF, 15: 704; Villiers, 1950, Initiations II, Serp. Ouest Afr. IFAN: 74, fig. 84; Manacas, 1957, An. Junta Invest. Ultramar, 10 (4, F.1): 14, Marques Mano, Ponta de Machado (Portuguese Guinea).

Lycophidion intermediates between *Lycophidion capense* and *acutirostre* Loveridge (part), 1933, Bull. Mus. Comp. Zool., 74: 234, Zanzibar (in error).[1]

Diagnosis. Two or three apical pits. Snout shorter than parietals. Postnasal in contact with 2nd labial, seldom with 1st as well. Scale rows 17–17–17 (rarely 15) in front of the anus. Ventrals: 165–187 (♂ ♂), 164–189 (♀ ♀). Subcaudals: 37–53 (♂ ♂), 30–44 (♀ ♀). Color brownish, finely

[1] Citations of *L. capense* by many authors, i.e. Bocage, Sjöstedt, Chabanaud, Angel, Leeson, Braestrup, Villiers, Monard, Cozens and Marchant, actually refer to *irroratum* and *semicinctum*, but this problem cannot be solved without an actual examination of the specimens.

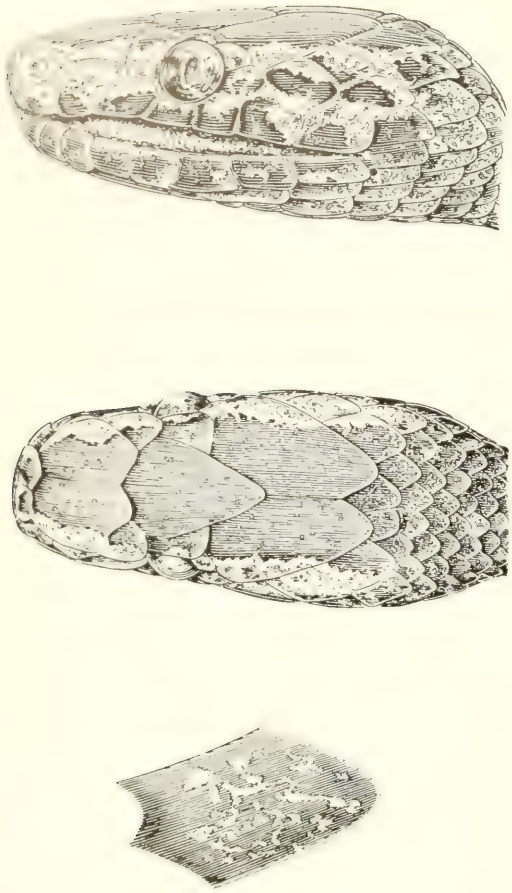

Figure 5. Lateral and dorsal views of head, and dorsal view of *L. ornatum*.

light stippled, a white band around the snout. Alternating dark spots in juveniles.

Maximum size observed (in mm). 325 (tail 41) in males; 440 (tail 50) in females.

Specimens examined. Sierra Leone: (FMNH 121979–80); *Liberia*: Monrovia (MCZ 916); Peatach, St. Paul's River (MCZ 22610); Mulhenberg Mission (USNM 22829). *Ghana*: Achimota School (MCZ 53641); Legon Hill near Achimota School (MCZ 53678); Kumasi (MCZ 49606, 49733); Oda (FMNH 4418, 53638); near Somanya (MCZ 55364). *Togo*: Warawara (MCZ 55360). *No locality*: (Zanzibar, in error) (MCZ 5992).

Lycophidion semicinctum Duméril and Bibron

Lycophidium semicinctum Duméril and Bibron, 1854, Herpet. Gen. 7: 414 (locality?). Angel, 1933, Bull. Com. Etud. Hist. Scient. AOF, 15: 705, fig. 32; Villiers, 1950, Initiations II, Serp. Ouest Afr. IFAN: 74, fig. 85; Manacas, 1957, An. Junta Invest. Ultramar, 10 (4, F.1): 15, Bissalanca, Marques Mano, Bissau (Portuguese Guinea).[2]

Diagnosis. Only one apical pit. Snout about as long as or longer than parietals. Postnasal in contact with 2nd labial, seldom with 1st as well. Scale rows 17–17–15. Ventrals: 183–193 (♂♂), 196–211 (♀♀). Subcaudals: 47–58 (♂♂), 36–46 (♀♀). (Exceptionally, 177 ventrals and 42 subcaudals in a male from northern Ghana—a fact which suggests a northern subspecies or a cline.) Color pattern with transverse bands or alternating spots, becoming indistinct in the largest specimens[3] without white stippling.

Maximum size (in mm): 478 (tail 88) in males; 788 (tail 88) in females.

Specimens examined. Portuguese Guinea: Bissau (MCZ 18192). *Ghana*: without locality (FMNH 74832); vicinity of Achimota School (MCZ 55365–71); near hospital, Achimota School (MCZ 53679–80); Achimota (MCZ 53677); Legon Hill near Achimota School (MCZ 55361, FMNH 74823–24); Lawra (MCZ 49560); near Somanya (MCZ 55362–63). *Cameroon*: Poli (MCZ 44130).

Lycophidion ornatum Parker

Lycophidion ornatum Parker, 1936, Novit. Zool., 40: 122, Congulu (Angola) and numerous localities in Congo, Tanzania, Burundi, Rwanda and Uganda; Witte, 1941, Explor. Parc Nat. Albert, 33: 179, numerous localities of Kivu (Congo) and Rwanda; Laurent, 1956, Ann. Mus. Roy. Congo Belge, Zool., Ser. 8, 48: 116, pl. XII, fig. 4, numerous localities in eastern Congo, Rwanda and Burundi.

Lycophidion capense capense (non A. Smith) Loveridge (part) 1936a, Field Mus. Nat. Hist., 22: 23, Ruchuru (Congo); Loveridge (part) 1936b, Bull. Mus. Comp. Zool., 79: 241, Kigezi Distr., Sipi (Uganda), Kaimosi (Kenya).

[2] See footnote under *L. irroratum*.

[3] These have been misidentified as *L. capense* or *L. ornatum*.

Lycophidion capense uzungwensis (non Loveridge) Witte (part) 1941, Explor. Parc Nat. Albert, 33: 178, Kiniha (Congo).

Lycophidion capense ornatum Loveridge, 1942, Bull. Mus. Comp. Zool., 91: 266, Bugoye, Nyakabande, Mushongere (Uganda), Idjwi Island (Congo), Ujiji (Tanzania).

Diagnosis. Only one apical pit. Snout shorter than the parietals. Postnasal in contact with 2nd labial, seldom with 1st as well. Scale rows 17–17–17. Ventrals: 183–206 (♂♂), 188–212 (♀♀). Subcaudals: 41–53 (♂♂), 36–46 (♀♀).

Brownish, each individual scale white stippled. A light band not only around the snout, but behind the eyes in the temporal region as well.

Maximum size observed (in mm): 443 (tail 66) in males, 558 (tail 63) in females.

Specimens examined. Sudan: Gilo (FMNH 62307). *Congo*, Kivu: Ruchuru (FMNH 12842); Lulenga (MCZ 24741–42); *Rwanda*: Upper Mulinga, Idjwi Island (MCZ 48193–249, FMNH 35308). *Uganda*: Muko, Lake Bunyoni (MCZ 42686, paratype, collected by C. R. S. Pitman); Nyakabande (MCZ 48303); Kigezi District (MCZ 39966); Bugoye (MCZ 48191); Gulu, Acholi (MCZ 47827); Sipi, Mt. Elgon (MCZ 40468–70). *Kenya*: Kakamega (MCZ 40471–73). *Tanzania*: Ujiji (MCZ 48250). *Uganda*: Lake Mutanda (MCZ 48192).

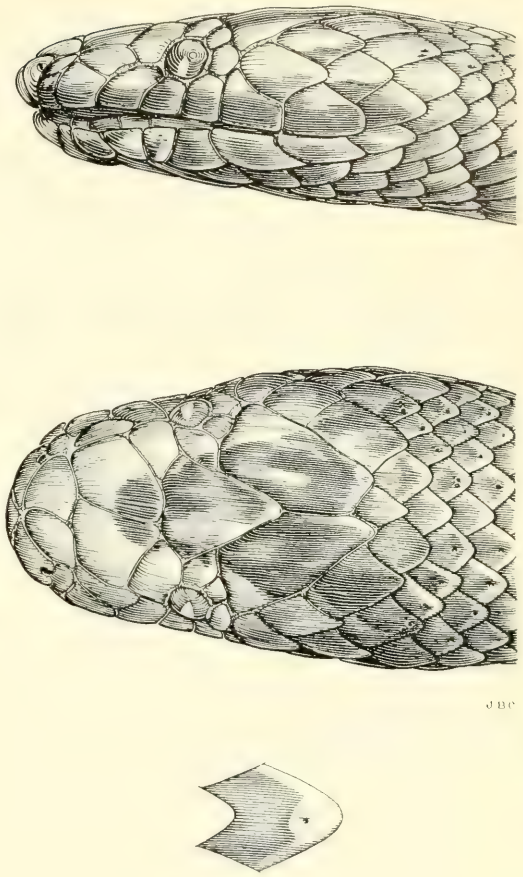

Figure 6. Lateral and dorsal views of head, and dorsal scale of *L. uzungwense*.

Lycophidion uzungwense Loveridge

Lycophidion capense uzungwensis Loveridge, 1932, Bull. Mus. Comp. Zool., 72: 375, Dabaga, Kigoga (Tanzania); Loveridge, 1933, Bull. Mus. Comp. Zool., 74: 235.

Diagnosis. Only one apical pit. Snout shorter than the parietals. Postnasal in contact with *both* 1st and 2nd labials. Scale rows 17–17–17. Ventrals: 180 (♂), 194 (♀). Subcaudals: 31 (♂), 23 (♀).

Brownish, each individual scale with a large white apical spot; a very broad white band around the snout and on the temporal region.

Size (in mm): 214 (tail 24) male (holotype); 272 (tail 23) female (paratype).

Specimens examined. Tanzania: Dabaga (MCZ 30117, holotype, collected by A. Loveridge 1.i.30); Kigogo (MCZ 30118, paratype, collected by A. Loveridge 22.i.30).

Lycophidion semiannule (Peters)

Lycophidium semiannulis Peters, 1854, Monatsber, Akad. Wiss. Berlin: 622, Tete (Mozambique).

Lycophidium acutirostre Günther, 1868, Ann. Mag. Nat. Hist., (4) 1: 427, pl. XIX, fig. D, Zanzibar (in error).

Lycophidion semiannule Laurent, 1964, Publ. Cult. Diamang, Mus. Dundo, 67: 97, Porto Amelia (Mozambique).

Diagnosis. Only one apical pit. Snout shorter than the parietals. Postnasal in contact with both 1st and 2nd labials.

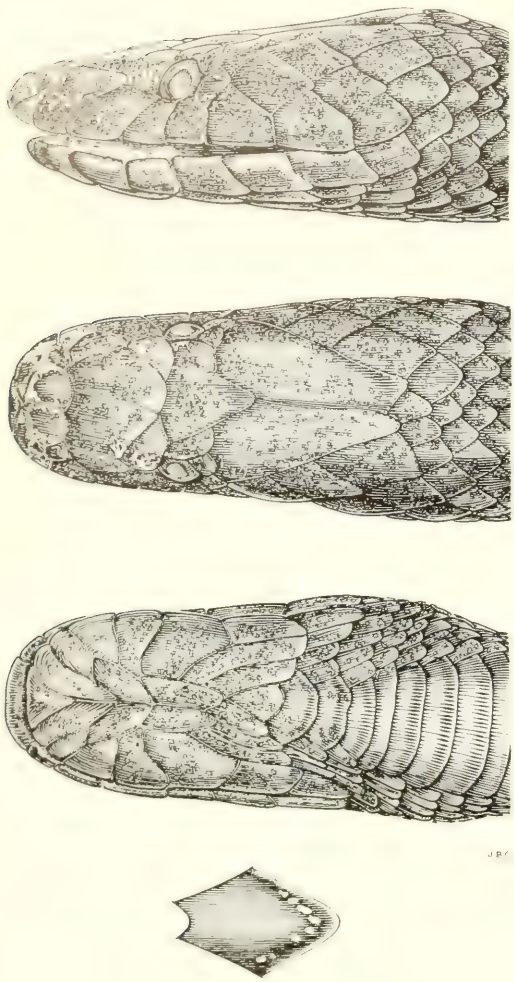

Figure 7. Lateral and dorsal views of head, and dorsal scale of *L. depressirostre*.

Scale rows 17–17–15. Ventrals: 134–148 (♂♂), 144–168 (♀♀). Subcaudals: 27–31 (♂♂), 18–30 (♀♀).

Brownish, the individual scales generally white stippled or white bordered. A broad white band with sinuous border around the head. Belly and throat dark.

Maximum size observed (in mm): 253 (tail 44) in males, 243 (tail 29) in females.

Specimens examined. Tanzania: Liwale (FMNH 81084). *Mozambique*: Lumbo (MCZ 18188–89; AMNH 16880; USNM 62900). *No locality* ("Zanzibar" in error): (BM 68–2–29–126, probably one of the syntypes of *L. acutirostre*). *Zambia*: Barotseland: Siholi Mission (FMNH 134259). *Rhodesia*: Bulawayo: (FMNH 121816).

Remarks. The specimen from Zambia differs from the others in its color pattern (transverse dark spots, light belly) and its high number of ventrals (168 instead of 144 in the only other female here considered). While it probably belongs to the species, it proves at least a geographical variation, but we have no clue to decide if a cline or a subspecies is involved.

Lycophidion depressirostre sp. n.

Lycophidium jacksoni Boulenger (part), 1893, Cat. Snakes Brit. Mus., 1: 340, Lamu Island (Kenya).

Lycophidium acutirostre (non Günther), Sternfeld 1912, Wiss. Ergebn. Deutsch Zentral Afrika Exp., 4: 268, Kenya; Boettger, 1913, *in* Voeltzkow, Reise in Ostafrika, 3, pt. 4: 363, Mavene (Tanzania).

Lycophidion capense capense (non A. Smith) Loveridge (part), 1933, Bull. Mus. Comp. Zool., 74: 233, Kampala (Uganda); Loveridge (part), 1951, Bull. Mus. Comp. Zool., 106: 188, Mgulani (Tanzania); Loveridge (part), 1956, Sudan Notes and Records, 36: 7, Torit (Sudan).

Lycophidion intermediates between *capense* and *acutirostre*, Loveridge (part), 1933, Bull. Mus. Comp. Zool., 74: 234, Bagamoyo, Kilosa, Morogoro (Tanzania).

Lycophidion capense >< *acutirostre* Loveridge, 1936, Bull. Mus. Comp. Zool., 79: 242, Kibwezi, Mt. Mbololo, Malindi, Changamwe (Kenya); Loveridge, 1942, Bull. Mus. Comp. Zool., 91: 269, Ugano, Mbanja (Tanzania).

Lycophidion capense uzungwense (non Loveridge) Bogert, 1941, Bull. Amer. Mus. Nat. Hist., 77: 31, Sankuri (Kenya).

? *Lycophidion capense* (non A. Smith) Parker (part), 1949, Zool. Verhand., 6: 54, Haud (Somali Rep.).

Holotype: MCZ 53348, Torit, Sudan, collected by John Owen 20.v.50.

Paratypes: Torit, Sudan (MCZ 53347, 53350, 53352, 53354–57; FMNH 58414, 62338–40), collected by John Owen 30.iv.50, 29.vi.59, vii. 50, 14.vi.48, 28.iii.50 and 22.iv.50. Yei, Sudan (FMNH 58321), collected by R. Alison 29.iv.48.

Diagnosis. Only one apical pit. Snout shorter than the parietals. Postnasal in

contact with *both* 1st and 2nd labials. Scale rows 17–17–15. Ventrals: 155–174 (♂♂), 161–178 (♀♀). Subcaudals: 32–39 (♂♂), 22–31 (♀♀).

Brownish, each individual scale with a light subapical spot generally *divided* in minute dots. No markings on the top plates of the head, but a broad, conspicuous light band with sinuous border around the snout. Belly and throat pigmented.

Maximum size observed (in mm). (a) In Sudanese populations: 362 (tail 50) in males, 492 (tail 42) in females. (b) Kampala specimen (♂): 362 (tail 52). (c) East African populations: 329 (tail 46) in males, 399 (tail 49) in females.

Other specimens examined. Uganda: Kampala (MCZ 30115). *Kenya*: Mtoto Andei (USNM 48590); Mt. Mbololo (MCZ 40480); Malindi (MCZ 40481); Kibwezi (MCZ 40478); Sankuri (AMNH 50792); Killibasi (AMNH 61661); Shaffa Dikka (AMNH 61644); Kaimosi (USNM 49388). *Tanzania*: Morogoro (MCZ 18495; AMNH 16881, 16883); Mgulani (MCZ 50289); Ugano (MCZ 44112); Bagamoyo (MCZ 30104–06); Kilosa (MCZ 18191); Mbanja (MCZ 48271); Liwale (MCZ 52641, 59178; FMNH 81089, 81695); Tunduru (MCZ 52642); Nachinzwea (FMNH 78207, 78209, 78214–15). *Somali Republic*: (BM 1949–2–1–80–82).

Geographical variation. Although the species is here described as monotypic, it is far from devoid of geographical variation. We already saw that the size is considerably smaller in the eastern populations.

In the Kampala specimen, the snout band is less wide and interrupted; the dorsal scales have a single apical spot. In the Kenya specimens, there are tiny black dots and vermiculations within the light band, the top head plates may have light dots, and the dorsal scales have many small subapical white dots. The Tanzania specimens are very similar, but the spots on the dorsal scales are more numerous and farther inside the scale.

The Somali individual has the white snout band still more reduced and no light dots on the dorsal scales.

Generally, the median plates of the head (internasals, prefrontals, frontal, supraoculars, parietals) are uniform; only seldom do they have a few light dots.

For the present, these variations are not considered worthy of any taxonomic recognition.

Lycophidion capense A. Smith

See synonymy and references under subspecies.

Species diagnosis. Only one apical pit. Snout shorter than parietals. Postnasal in contact with *both* 1st and 2nd labials. Scale rows 17–17–15. Ventrals: 166–211 (♂♂), 173–219 (♀♀). Subcaudals: 31–58 (♂♂), 24–44 (♀♀). Brownish in general, with each individual scale showing a single large subapical white spot. Head plates with or without light vermiculations. Belly dark or light but throat generally light.

Lycophidion capense capense Smith

Lycodon capense A. Smith, 1831, S. African Quart. Jour., (1) 5: 18, Kurrichane, i.e. Rustenberg Distr. (Transvaal).

Lycodon horstoki Schlegel, 1837, Essai Phys. Serp., 2: III, pl. IV, figs. 10–11, Cape of Good Hope.

Lycophidion capense capense Bogert (part), 1940, Bull. Amer. Mus. Nat. Hist., 77: 30, Merebank (Natal); FitzSimons, 1962, The Snakes of Southern Africa: 124, many localities listed.

Diagnosis: Ventrals: 180–188 (♂♂), 188–190 (♀♀). Subcaudals: 36–41 (♂♂), 30–39 (♀♀). Brownish above, each individual scale showing a single large subapical white spot (which can be irregular in shape) or several smaller dots or a white apical border. Head plates with light vermiculations. Belly and throat entirely light colored.

Maximum size observed (in mm). 325 (tail 45) in only 3 males available.

Specimens examined. Transvaal: Pretoria (MCZ 14193). *Natal*: Ottawa (AMNH 5903); Merebank (AMNH 60109). *Cape Colony*: Grahamstown (MCZ 21482).

Remarks. The number of specimens examined is admittedly too few. Therefore, the diagnosis and the range of the typical form of the species must be considered as very tentatively outlined here.

Range. South Africa, surely from Cape Colony to Natal and Transvaal, but the northern limits (Zambeze or Limpopo?), if not arbitrary, are still not known.

Lycophidion capense multimaculatum Boettger

Lycophidium capense, mut. *multimaculata* Boettger, 1888, Ber. Senckenb. Naturf. Ges., 67, Povo Nemlao, Povo Netonna (Lower Congo).

Lycophidium capense Bocage, 1895, Herp. Angola: 81, Caconda, Galanga, Mossamedes, "Angola" (Angola).

Lycophidion capense capense (non A. Smith) Schmidt, 1933, Ann. Carnegie Mus., 22: 13, Chitau, Gauca (Angola); Bogert (part), 1940, Bull. Amer. Mus. Nat. Hist., 77: 30, "Angola"; Mertens (part), 1955, Abhandl. Senckenb. Naturf. Ges., 490: 92, Gammans, Okahandja, Grootfontein (Southwest Africa).

Lycophidion capense multimaculatum Laurent, 1956, Ann. Mus. Roy. Congo, in 8°, Zool., 48: 115, Penemende, sources of the Lofoi, Niemba-Lukuga confluent (southeastern Congo); Laurent, 1964, Publ. Cult. Diamang, Mus. Dundo, 67: 94, Dundo, Alto Cuilo, Cazombo, Macondo, Calonda (Angola).

Diagnosis. Ventrals: 167–180 (♂♂), 173–184 (♀♀). Subcaudals: 31–42 (♂♂), 24–37 (♀♀). Brownish above, each individual scale bearing a single subapical light spot, sometimes irregular or divided, sometimes replaced by scattered light spots. Head plates with light vermiculations in southern populations, becoming uniform or with only a line around the snout in northern populations. Belly light in southern populations, dark in northern populations, partly pigmented in intermediate populations. Throat always light.

Maximum size observed (in mm). 358 (tail 45) in males, 527 (tail 54) in females.

Specimens examined. Southwest Africa: Okamandja (FMNH 57653, 62780, 64482, 65870, 81618); Luderitz Bay (MCZ 22050). *Bechuanaland*: Maun (FMNH 17722). *Rhodesia*: Bembezi (USNM 142081); Bulawayo (MCZ 12620, 56349, 58188–90); Chirinda (MCZ 29177–78). *Zambia*: Kalichero (MCZ 69048); Msuro (MCZ 69049); Abercorn (MCZ 54657–59). *Angola*: no precise locality (AMNH 50511); Chitan (FMNH 18524); Lundo (MCZ 74128).

Range. From Southwest Africa and Rhodesia to southern Congo.

Remarks. The populations united under this trinomen are obviously very diverse. It has been assumed that this variation is clinal but this remains to be confirmed, as does the non-clinal nature of the transition with the typical form. The southern populations of *multimaculatum* have lower ventral counts than *L. capense capense*, but they keep their characteristic color pattern, namely the light belly. It seems that this character evolves clinally in a northern direction. The head reticulations disappear in northern populations (northern Angola and southern Congo). The specimens from Abercorn have white stippled dorsal scales, as are common in *L. depressirostre*; the others have the single spot which appears characteristic of the species in Central Africa. The relationships of the *multimaculatum* populations with forms to the east are unclear. My investigations in the eastern Congo have definitely shown that no smooth transition exists between *multimaculatum* and *jacksoni*.

A last point must be mentioned here: the specimen from Angola (AMNH 50511) has the striking color pattern of *L. hellmichi*, but the scale counts of *multimaculatum*. It appears that more samples from southern Angola are badly needed for a proper evaluation of the situation.

Lycophidion capense jacksoni Boulenger

Lycophidium jacksoni Boulenger (part), 1893, Cat. Snakes, Brit. Mus., 1: 340, pl. XXI, fig. 3, Kilimanjaro (Tanganyika = Tanzania).

Lycophidium abyssinicum Boulenger, 1893, Cat. Snakes, Brit. Mus., 1: 342, pl. XXII, fig. 1, southern Abyssinia.

Lycophidion irroratum (non Leach) Schmidt, 1923, Bull. Amer. Mus. Nat. Hist., 23: 68, Dungu, Garamba (northeastern Congo).

Lycophidion capense capense (non A. Smith) Loveridge (part), 1933, Bull. Mus. Comp. Zool.,

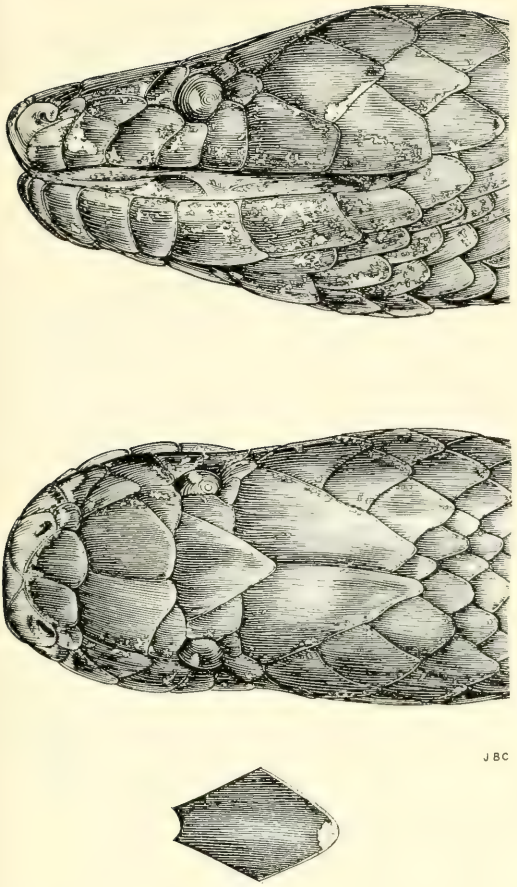

Figure 8. Lateral and dorsal views of head, and dorsal scale of *L. capense jacksoni*.

74: 233, Ujiji (Tanzania), Ukerewe Island (Lake Victoria), Jinja (Uganda); Loveridge (part), 1936, Field Mus. Nat. Hist., Zool., 22: 23, Nairobi (Kenya), Harar (Ethiopia), "Belgian Congo"; Loveridge (part), 1936, Bull. Mus. Comp. Zool., 79: 241, Sabei (Uganda); Uthmöller, 1937, Temminckia, 2: 107, Gomberi, Sanya (Tanzania); Uthmöller, 1941, Zool. Anz., 135: 233, Gomberi, Hanang, Momella, Mtowa-mbu, Sanya, Yaida; Witte, 1941, Explor. Parc Nat. Albert, 33: 178, Kalinga, Mabenga (eastern Congo), Nyakatare (Rwanda); Loveridge (part), 1942, Bull. Mus. Comp. Zool., 91: 268, Butiaba (Uganda); Ujiji (Tanzania); Loveridge (part), 1956, Sudan Notes and Records, 36: 7, Gilo Imurok, Latome, Nimule, Tarangole, Yegiyegi (Sudan).

Lycophidion capense uzungwensis (non Loveridge) Witte (part), 1941, Explor. Parc Nat. Albert, 33: 178, Kanyabayongo (eastern Congo).

Lycophidion capense jacksoni Laurent, 1956, Ann. Mus. Roy. Congo, in 8°, Zool., 48: 109, pl. XII, fig. 3, numerous localities of eastern Congo, Rwanda and Burundi; Skelton-Bourgeois, 1961, Rev. Zool. Bot. Afr., 63: 333, Ngorongore, Hanang, Marangu (Tanzania).

Diagnosis. Ventrals: 178–192 (♂♂), 184–206 (♀♀). Subcaudals: 34–45 (♂♂), 28–38 (♀♀). Brownish above, each individual scale with a single subapical light spot or a light border. Head plates almost always without light markings on the top, generally with only a slender white line around the snout. Belly dark, but throat light.

Maximum size observed in specimens cited (in mm). 424 (tail 53) in males, 535 (tail mutilated 30) in females (see also Laurent, 1956 and 1960).

Specimens examined. Tanzania: Tumba, Lake Rukwa (MCZ 54654–56); Kibondo (MCZ 51626); Igala, Kigoma (MCZ 54817); Ujiji (MCZ 30113, 48252–53); Ukerewe Id., Lake Victoria (MCZ 30114). *Kenya*: without locality (USNM 42049); Maima Springs (FMNH 79146); Kijabe (FMNH 2430); Parklands (MCZ 18190); Lat. 0°, Long. 39°E (MCZ 11485); Nairobi (USNM 40966–67); Wambugu (USNM 40885); between Mt. Kenya and Fort Hall (USNM 41133); Lake Sirgoit (USNM 42023); between *Abyssinia and Kenya* (USNM 66928). *Uganda*: Buddu Coast (AMNH 5259, 24284); Nyenga (AMNH 63770–72); Jinja (MCZ 30116); Sebei, Mt. Elgon (MCZ 40467); Butiaba Swamp, Lake Albert (MCZ 48251). *Congo*: without locality (FMNH 4027); Bunia (MCZ 25149); Garamba (AMNH 12035); Dungu (AMNH 12041). *Sudan*: Gila, Imatong Mountains (MCZ 53342); Imurok (MCZ 53343); Juba (FMNH 58500, 58510); Katire (FMNH 62308); Latome (MCZ 53344); Nimule (MCZ 53345); Terangore (MCZ 53346); Torit (MCZ 53349, 53351, 53353); Yei (FMNH 58322). *Ethiopia*: Harrar (FMNH 4026).

Range. Sudan and western Ethiopia to southern Kivu and western Tanzania through Uganda, western Kenya, Rwanda and Burundi.

Remarks: It has been established beyond any reasonable doubt that *jacksoni* does not merge into *multimaculatum* in the Congo, the Fizi escarpment being the very sharp limit between the two races. That a clinal transition does not exist at the eastern side of Lake Tanganyika cannot be proved with the available data; there is, on the contrary, a clinal suggestion in the relatively low ventral counts of the Lake Rukwa specimens. The range of this subspecies is large since specimens from Sudan and even from Abyssinia are not separable from it. The type of *abyssinicum* proves to be a synonym of *jacksoni*.

Lycophidion capense subsp.

Lycophidion capense (non A. Smith) Parker (part), 1949, Zool. Verhandl., 6: 54, Borama Distr., Haud (Somalia), Waramalka (Ethiopia).

Diagnosis. Ventrals: 166–175 (♂♂), 177–188 (♀♀). Subcaudals: 34–35 (♂♂), 26–32 (♀♀). Brownish, each dorsal scale with a subapical light spot or with scattered small subapical dots. Head markings as in *jacksoni*, sometimes (2 specimens) with light punctation and vermiculations on the crown plates. Belly dark and throat generally dark also. A white collar in some specimens.

Maximum size observed in specimens examined (in mm). 309 (tail 34) in males, 463 (tail 48) in females.

Specimens examined. *Ethiopia*: Ouaramalka (BM 1916-6-24-4-5). *Somali Republic*: Haud (BM 1949-2-1-72, 1949-2-1-78–79, 1949-2-1-83); Borama (1955-1-11-33).

Range: Northern Somali Republic and adjacent parts of Ethiopia.

Remarks. The eastern Ethiopian and Somalian populations appear to represent an undescribed subspecies. The ventral and subcaudals differ somewhat from the *jacksoni* counts and are not very much higher than the *multimaculatum* counts. These populations differ from *multimaculatum* by their generally dark throat, and from both *jacksoni* and *multimaculatum* by the presence of a white collar in some specimens. However, we do not name this suspected subspecies, because the apparent variability of this small sample is such that we are not quite sure that it is really homogeneous. Furthermore, the data are too scant to suggest unequivocally the absence of a clinal transition with *jacksoni*.

Lycophidion capense loveridgei subsp. n.

Lycophidion capense Barbour and Loveridge, 1928, Mem. Mus. Comp. Zool., 50: 113, Bagilo, Nyange, Vituri, Ulurungu Mountains; Amani, Bumbuli, Usambara Mountains.

Lycophidion capense capense (non A. Smith) Loveridge (part), 1933, Bull. Mus. Comp. Zool., 74: 233, Mwaya, Lake Nyasa (Tanzania); Loveridge (part), 1936, Bull. Mus. Comp. Zool., 79: 241, Mkonumbi, Ngatana (Kenya); Loveridge (part), 1942, Bull. Mus. Comp. Zool., 91: 268, Amboni Estate (Tanzania), Kilindini (Kenya).

Holotype: 1 ♀ (MCZ 23196), Amani, Usambara Mountains, Tanzania, collected by A. Loveridge 29.xi.26.

Paratypes: 1♂, 1♀ (MCZ 23197–98), Amani, Usambara Mountains, Tanzania, collected by A. Loveridge 29.xi.26.

Diagnosis. Ventrals: 193–211 (♂♂), 205–219 (♀♀). Subcaudals: 47–58 (♂♂), 38–44 (♀♀). Brownish on the back, each individual scale with a subapical white spot or a white border. Head plates with many light dots or vermiculations. Belly dark, with a light throat.

Maximum size observed (in mm). 480 (tail 80) in males, 623 (tail 73) in females.

Other specimens examined. *Kenya*: Mkonumbi 1♀ (MCZ 40474); Ngatana, 1♀ (MCZ 40475); Likoni, mainland opposite Kilindini, 1♂ (MCZ 48266). *Tanzania*: Amboni Estate, 2♂♂ (MCZ 48264–65); Usambara Mountains, Bumbuli, 1♂ (MCZ 23200); Uluguru Mountains, Bagilo, 1♀ (MCZ 23189). Nyange, 1♂, 3♀♀ (MCZ 23190–93); Vituri, 1 juv. (MCZ 23195); Mwaya, Lake Nyasa, 1♂, 1♀ (MCZ 30109–10). *Zanzibar*: 1♀ (BM 1950-1-5-35).

Range and comments. This subspecies appears to live within a narrow band going from coastal Kenya in a southwest direc-

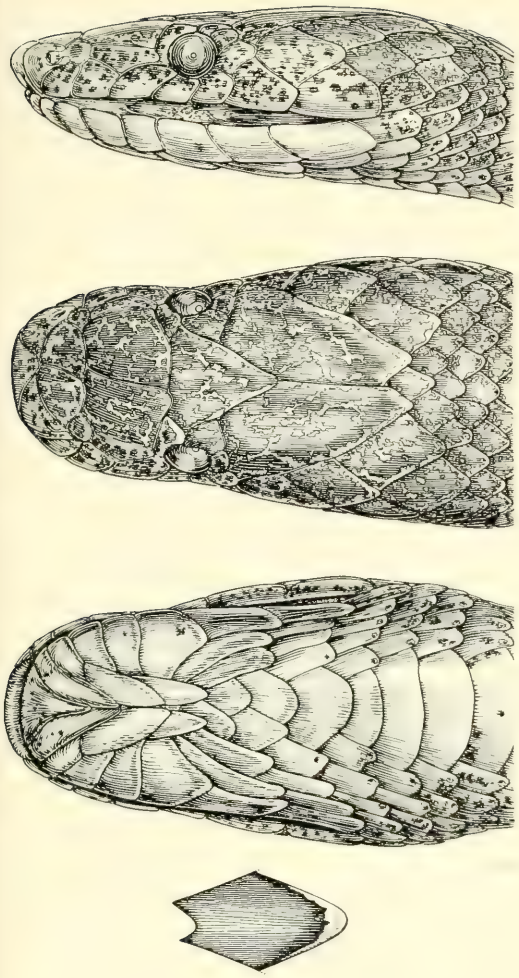

Figure 9. Lateral and dorsal views of head, and dorsal scale of *L. capense vermiculatum*.

tion to the northern shore of Lake Nyasa, through coastal northern Tanzania, Usambara and Uluguru Mountains. Nowhere do the *loveridgei* populations come near the known *jacksoni* localities, but even if the intervening space (between Kilimanjaro and the coast or between Lake Rukwa and Lake Nyasa) should be occupied by intermediary populations, the vastness of the *jacksoni* range hardly allows us to suppose that the race here described might be part of a smooth cline going from the Lake Victoria and Lake Tanganyika region towards the coast. Unfortunately, there is a very large blank in central Tanzania: we simply don't know what species of *Lycophidion* are living there.

Lycophidion capense vermiculatum subsp. n.

Lycophidion capense capense (non A. Smith) Bogert (part), 1940, Bull. Amer. Mus. Nat. Hist., 77: 30, Mlanje (Malawi); Loveridge (part), 1942, Bull. Mus. Comp. Zool., 91: 268, Mikindani, Mbanja, Nchingidi (Tanzania); Loveridge (part), 1951, Bull. Mus. Comp. Zool., 106: 188, Liwale (Tanzania); Loveridge (part), 1953, Bull. Mus. Comp. Zool., 110: 258, Kotakota, Cholo Mountains (Malawi); Manaças, 1959, Mem. Junta Invest. Ultramar, 8: 139, Vila Paiva de Andrada (Mozambique).

Holotype: 1♂ (MCZ 48225), Mbanja, near Lindi, Tanzania, collected by A. Loveridge 26–30.iv.29.

Paratypes: 1♂, 1♀ (MCZ 48256–57), Mbanja, near Lindi, Tanzania, collected by A. Loveridge 26–30.iv.29.

Diagnosis. Ventrals: 182–195 (♂♂), 192–203 (♀♀). Subcaudals: 43–52 (♂♂), 33–41 (♀♀). Color pattern as in *loveridgei*.

Maximum size observed (in mm). 385 (tail 61) in males, 521 (tail 57) in females.

Other specimens examined. Tanzania: Morogoro, 1♂, 1♀ (AMNH 16882, 16884); Mikindani, 1♂ (MCZ 48254); Nichingidi, Rondo Plateau, 3♂♂, 1♀ (MCZ 48260–63); Ruponda, 1♀ (MCZ 52640); Liwale, 7♂♂, 3♀♀ (MCZ 50249, 52639; FMNH 81083, 81085–88, 81693–94, 81696); Nachinzwea, 7♂♂, 3♀♀ (FMNH 78204–06, 78208, 78210–13, 78216, 81208). *Malawi*: Kotakota, 1♀ (AMNH 67793); Mlanje, 1♀ (AMNH 44308); Cholo Mountains; 1♀ (MCZ 51095).

Range. Southeastern Tanzania, Malawi and presumably northern Mozambique.

Comments. The difference in ventral counts between *vermiculatum* and *loveridgei* is clear cut enough to almost certainly preclude any clinal possibility. The lateral relationships with *multimaculatum* in North Rhodesia and with *capense* through southern Mozambique are unknown.

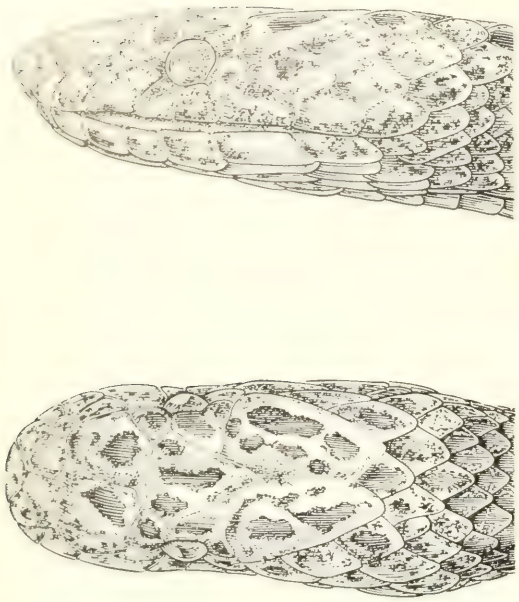

Figure 10. Lateral and dorsal views of head of *L. capense pembanum*.

Lycophidion capense pembanum subsp. n.

Lycophidion capense capense Moreau and Pakenham, 1941, Proc. Zool. Soc. London, Ser. A, 110 (parts 3 and 4): 108.

Holotype: 1 ♂ (BM 1940–1–18–74), Pemba Island.

Paratypes: 2 ♂♂ (BM 1940–1–18–75–76), Pemba Island; 1 ♀ (MCZ 46133), Wete, Pemba Island.

Diagnosis. Ventrals: 172 (♂ Holotype), 179–180 (♀♀). Subcaudals: 46 (♂), 37–40 (♀♀). Brownish on the back, each individual scale light bordered and/or with a subapical light spot. Head light colored with dark spots. Belly brown, throat light colored.

Size (in mm). Holotype (male): 267 (tail 53). The longest female (MCZ 46133) measured 406 mm (tail 51 mm).

Range. Pemba Island (Tanzania).

Comments. This insular subspecies is highly characteristic. No other *Lycophidion* has this very peculiar color pattern on the head, which is very similar to that of *Miodon collaris*. The ventral counts are somewhat lower than in the neighboring mainland populations (*vermiculatum* and *loveridgei*) but similar to those of *multimaculatum* or of the Somalian populations. The subcaudal counts are as in *vermiculatum* but somewhat lower than in *loveridgei*. The sharpness of the characters, as well as the geographical isolation, demonstrate that any clinal connection with other subspecies is out the question.

Key to the Recognizable Species and Subspecies in the Genus *Lycophidion*

Some species which in the past have been referred to *Lycophidion* are now attributed to other genera like *Oophilositum*, *Chamaelycus* (with which *Oophilositum* has been recently synonymized by de Witte, 1963), and *Dendrolycus*. They are, of course, not in this key, which is modified from that of Parker (1933).

1. Apical pits double or more. Scale rows 17, only rarely reduced in number before the vent 2
   Apical pits single 3
2. Apical pits 2 to 6, usually 4. Two labials only entering the eye. Rain Forest (West Africa to eastern Congo) ..... *L. laterale* Hallowell
   Apical pits 2, sometimes 3. Three labials entering the eye. West Africa ..... *L. irroratum* (Leach)[1]
3. Maximum number of scale rows 19. Two labials entering the eye. Congo forest ..... *L. polylepis* Boulenger
   Maximum number of scale rows 15 or 17. Three labials entering the eye 4
4. Maximum number of scale rows 15. From Angola to Tanzania ..... *L. meleagre* Boulenger
   Maximum number of scale rows 17 5
5. Scale rows generally not reduced in front of the vent. A broad ∩-shaped light band around the snout, still very wide and conspicuous in the temporal region .. 6
   Scale rows generally reduced in front of the vent. When present, light snout band narrow or, if broad, is disintegrating in the temporal region 7
6. Postnasal generally not in contact with the first labial. Subcaudals: 41–53 (♂♂), 36–46 (♀♀). Dorsal scales light stippled. Snout band less broad. Highlands of Central Africa, Sudan to Angola through eastern and southern

[1] A western and an eastern subspecies are perhaps recognizable on the basis of ventral and subcaudal counts in the males.

Congo, Uganda, Rwanda, Burundi and western Tanzania ..... *L. ornatum* Parker

Postnasal in contact with the first labial. Subcaudals: 31 (♂), 23 (♀). Dorsal scales with a single large white apical spot. Snout band broader than in any other form. Uzungwe Mountains ..... *L. uzungwense* Loveridge

7. Snout about as long or longer than parietals. Postnasal seldom in contact with first labial. West Africa ..... *L. semicinctum* Duméril and Bibron

Snout shorter than parietals. Postnasal generally in contact with first labials 8

8. Fewer ventrals and subcaudals. Ventrals: 134–174 (♂♂), 144–178 (♀♀). Subcaudals: 27–39 (♂♂), 18–31 (♀♀). Throat dark as the belly. A broad light band around the snout; generally no other head markings, except sometimes very inconspicuous light stippling on the top plates. Dorsal scales generally light stippled in the apical region, rarely with a single light spot or border 9

More ventrals and subcaudals. Ventrals: 166–211 (♂♂), 173–219 (♀♀). Subcaudals 31–58 (♂♂), 24–44 (♀♀). Throat light colored (except in some Ethiopian populations). Light band around the snout narrow or absent; when it is absent, light vermiculations generally present on top head plates; when it is present, the head plates are generally uniform. Dorsal scales generally with a single apical white spot or white border, rarely with light dots or vermiculations 10

9. Fewer ventrals and subcaudals (in males only). Ventrals: 134–148 (♂♂), 144–156 (♀♀), but 168 in one specimen with black annuli from Rhodesia (presumably a different subspecies). Subcaudals: 27–31 (♂♂), 18–30 (♀♀). Maximum size ± 25 cm. Southeastern Tanzania, Mozambique, Zambia ..... *L. semiannule* Peters

More ventrals and subcaudals (in males only). Ventrals: 155–174 (♂♂), 161–178 (♀♀). Subcaudals: 32–39 (♂♂), 22–31 (♀♀). Maximum size 36 cm (♂♂), 50 cm (♀♀). Sudan to southeastern Tanzania through Uganda and Kenya ..... *L. depressirostre* Laurent

10. Sides of the body (ventrals and 2 or 3 rows of dorsal scales) and sides of the head light colored; vertebral and paravertebral scales sometimes also light colored. More ventrals than the sympatric populations of *L. capense*: 197 (♂), 206–214 (♀♀). Southwestern Angola and southwest Africa ..... *L. hellmichi* Laurent

Sides of the body dark like the back; no light vertebral band. Fewer ventrals in South Africa, Angola, Rhodesia and Zambia: 167–188 (♂♂), 173–190 (♀♀) ..... *L. capense* 11

11. Generally no light band around the snout, but light vermiculations or small dots on the top head plates (prefrontals, frontal, parietals)[5] 12

Generally a narrow light band around the snout, but no light vermiculations or dots on the head plates 16

12. Fewer subcaudals, the difference being diagnostic in males: 31–42 (♂♂), 24–39 (♀♀). Belly generally light colored. Dorsal scales sometimes light stippled, although more generally with only a single spot or border of irregular outline 13

More subcaudals: 43–58 (♂♂), 33–44 (♀♀). Belly dark colored. Dorsal scales never light stippled, always with a single spot or border 14

13. More ventrals: 180–188 (♂♂), 188–190 (♀♀). More subcaudals in females: 30–39. Belly always light. Never a light line around the snout. South Africa ..... *L. capense capense* Smith

Fewer ventrals: 167–180 (♂♂), 173–184 (♀♀). Fewer subcaudals in females: 24–37. Belly sometimes dark and sometimes a light line around the snout without head vermiculations in northern populations. From southwest Africa to southern Congo through Angola, Bechuanaland, Rhodesia and Zambia ..... *L. capense multimaculatum* Boettger

14. Top of the head dark with light dots and vermiculations. More ventrals: 182–211 (♂♂), 192–219 (♀♀). Continental East Africa and Zanzibar 15

Top of the head light with dark spots. Fewer ventrals: 172 (♂), 179–180 (♀♀). Pemba Island ..... *L. capense pembanum* Laurent

15. Fewer ventrals: 182–195 (♂♂), 192–203 (♀♀). Fewer subcaudals: 43–52 (♂♂), 33–41 (♀♀). Southeastern Tanganyika to southern Malawi ..... *L. capense vermiculatum* Laurent

More ventrals: 193–211 (♂♂), 205–219 (♀♀). More subcaudals: 47–58 (♂♂), 38–44 (♀♀). Coastal Kenya to northern shore of Lake Nyasa through

[5] Exceptions make it useful to try both alternatives when the origin of the specimens is unknown or doubtful.

Tanganyika highlands
L. capense loveridgei Laurent

16. Fewer ventrals: 166–180 (♂♂), 173–188 (♀♀). Somewhat fewer subcaudals: 31–42 (♂♂), 24–37 (♀♀). Sometimes top head vermiculations present, as well as a light stippling on dorsal scales 17

More ventrals: 178–192 (♂♂), 184–206 (♀♀). Somewhat more subcaudals: 34–45 (♂♂), 28–38 (♀♀). Top head vermiculations very rarely, and light stippling on dorsal scales never present. Throat always light and belly always dark. From northwestern Tanzania to Sudan and western Ethiopia through northeastern Congo, Burundi, Rwanda, western Kenya and Uganda .....
L. capense jacksoni Boulenger

17. Throat light (belly light also in southern populations). Snout light line generally absent, top head plates generally with light vermiculations. Southern Congo, Angola and Zambia .... Northern populations of *L. capense multimaculatum* Boettger

Throat dark as well as the belly. Snout light line generally present; light vermiculations sometimes present on the top head plates. Somalia and eastern Ethiopia ..... *L. capense* subsp.

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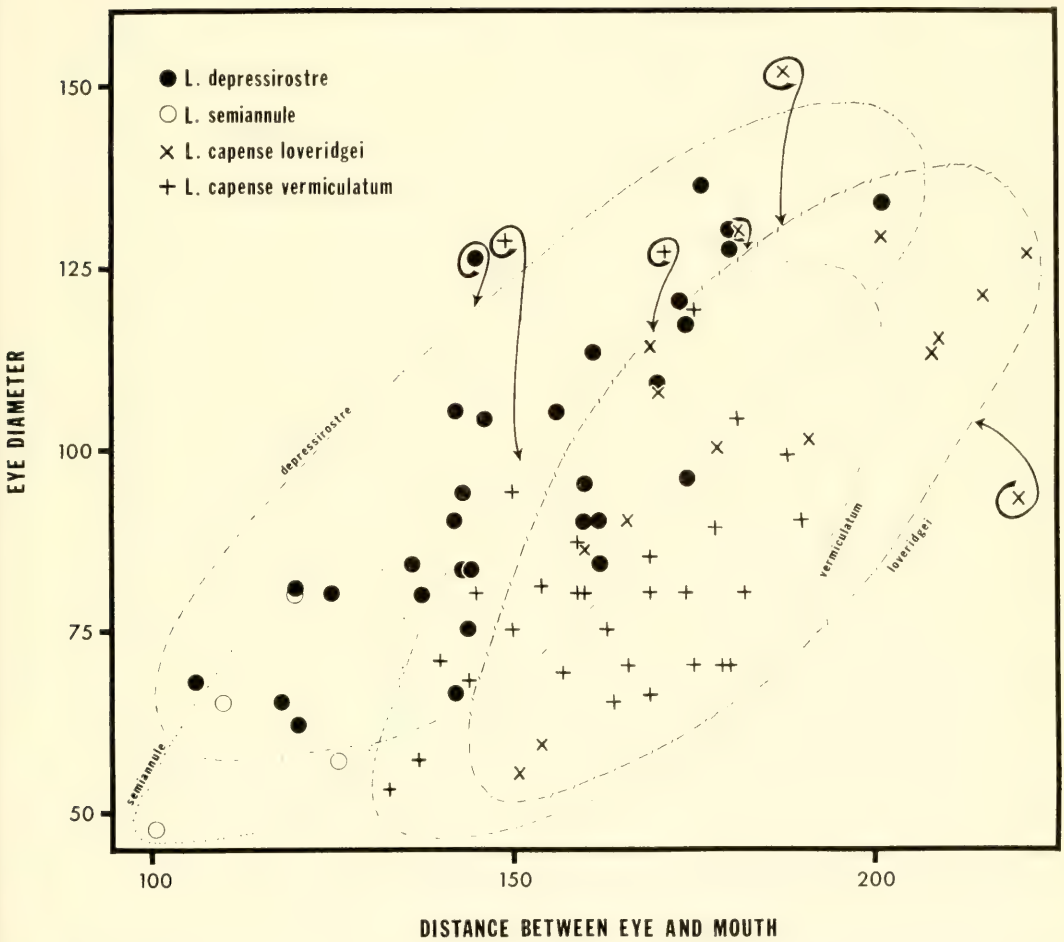

Figure 11. Eye diameter in relation to its distance from the mouth, in East African species of *Lycophidion*. This once allegedly key character is actually very poor.

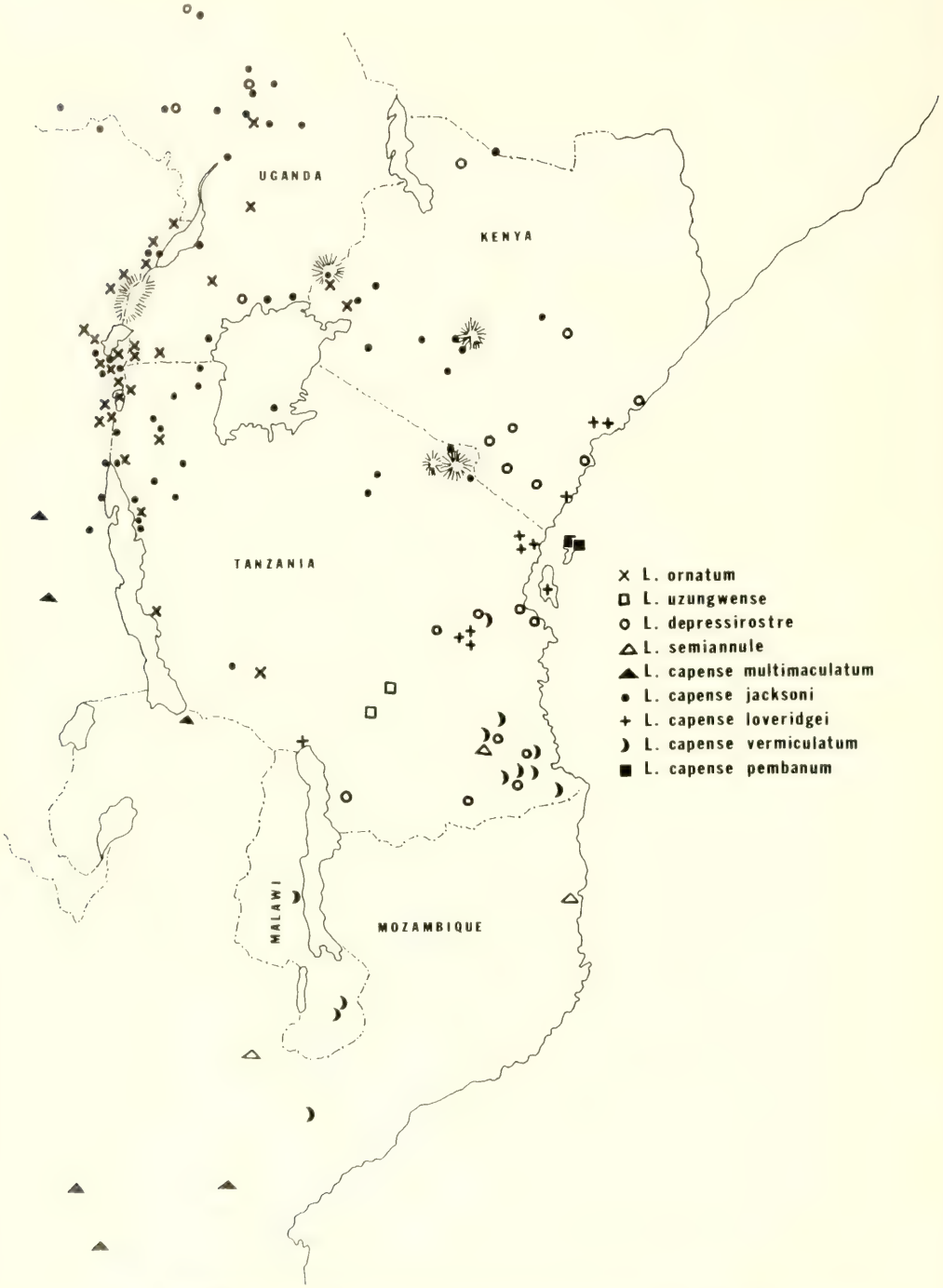

Figure 12. Range of the East African species and subspecies of the genus *Lycophidion*.

Bulletin OF THE
Museum of
Comparative
Zoology

Additional Scythian Ammonoids from Afghanistan

BERNHARD KUMMEL

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 136, NUMBER 13
MAY 29, 1968

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

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Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
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Cambridge, Massachusetts 02138, U. S. A.

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ADDITIONAL SCYTHIAN AMMONOIDS FROM AFGHANISTAN

BERNHARD KUMMEL

INTRODUCTION

The Lower Triassic formations and faunas of Afghanistan were essentially unknown until publication of the recent monograph by Kummel and Erben (1968). That report was based on field observations and collections made by H. K. Erben at Kotal-e-Tera, near the village of Altimur, 90 kilometers southeast of Kabul, Afghanistan (Fig. 1). In that monograph the Triassic section at Kotal-e-Tera was shown to consist of a relatively thin, gray limestone unit containing an ammonoid fauna of mid-Scythian (*Owenites* Zone) age. This gray limestone sequence overlies dolomites of Permian age and is overlain by black limestones that contain ammonoids of Anisian age.

In August of 1966 I had the opportunity to visit Kotal-e-Tera and make additional observations and collections on these Triassic formations. The most important result from the visit was the discovery in the uppermost part of the lower Triassic (Scythian) limestone formation of a *Subcolumbites* fauna of late Scythian age. The paper by Kummel and Erben was submitted in November, 1964, and was in press, thus this new information is presented here as a separate contribution.

ACKNOWLEDGMENTS

It gives me great pleasure to acknowledge the warm hospitality and help given me by Dr. Klaus P. Vogel, Chief of the Bonn University Geological Mission to the University of Kabul. Professor H. K. Erben of Bonn University kindly helped in preliminary arrangements for my visit. I was very ably assisted in the field by Mr. K. Azizullah Kureishie, a graduate student in geology at the University of Kabul. My trip was made possible by a generous grant from the Shaler Fund of Harvard University. Miss Victoria Kohler aided in the preparation, photography, and illustrations of the specimens, with her usual good will and skill. The laboratory aspects of this study were supported by National Science Foundation grant GB-5109X.

STRATIGRAPHY

Triassic formations crop out extensively in the general region of the village of Altimur and around Kotal-e-Tera. The road from Kabul to Gardez (12 kms south of Altimur) crosses the main band of outcrops. There is an excellent exposure of the Permian and Triassic formations on the east side of the Kabul-Gardez road. At this outcrop I was able to measure the following section (Fig. 2):

K7.	Mudstone, black, calcareous, contains abundant ammonoids which, however, generally cannot be extracted. Unit overlain by alluvium, thickness given is only that of beds exposed.	50 feet
K6.	Limestone, light to dark	

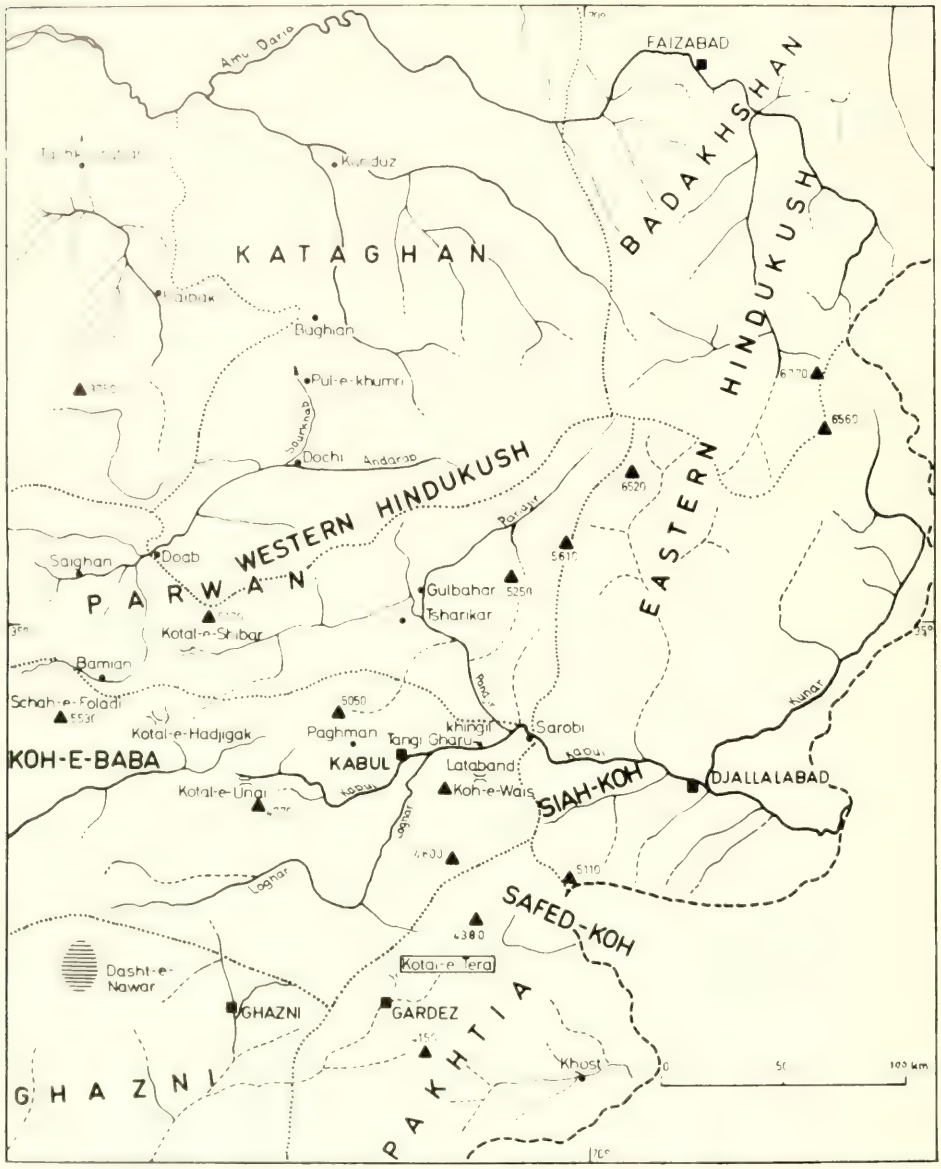

Figure 1. Locality map of northeastern Afghanistan showing location of Kotal-e-Tera.

gray, made up of shell fragments, matrix of fine-grained calcite, unit very hard; contains abundant ammonoids but preservation poor and very difficult to extract. 11

K5. Limestone, red, massive, very fine grained, dolomitic in patches, with abundant shell fragments; contains ammonoids but these are difficult to extract from the rock. 1

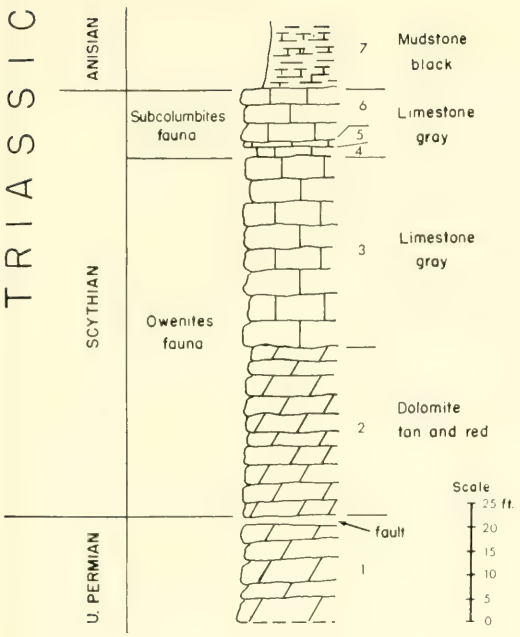

Figure 2. Columnar section of uppermost Permian and Triassic strata cropping out along the east side of the Kabul-Gardez road at Kotal-e-Tera.

K4. Limestone, gray, made up of shell fragments, with very fine-grained matrix, thin bedded, unit weak, no fossils seen. 2

K3. Limestone, gray, made up of shell fragments with very fine- to fine-grained matrix, partly dolomitic; contains abundant ammonoids. 40

K2. Dolomite, buff to gray, fine- to medium-grained, upper part red in color; contains abundant ammonoids. 35

K1. Dolomite, gray, massive, no fossils seen, unit poorly exposed. 16

Bed K1 of the above section is just the upper part of the Permian formations exposed at Kotal-e-Tera and is in fault contact with bed K2. The *Owenites* fauna described by Kummel and Erben (1968) is present in beds K2 and K3. From this outcrop and from that on the west side of the Kabul-Gardez road, Kummel and Erben (1968) recognized the following species of ammonoids:

Pseudosageceras multilobatum Noetling
Subinyoites cf. *kashmiricus* (Diener)
Subvishnuites welteri Spath
Xenodiscoides cf. *falcatum* (Waagen)
Dieneroceras knechti (Hyatt and Smith)
Clypeoceras yudishthira (Diener)
Eoptychites sp. indet.
Owenites koeneni Hyatt and Smith
Owenites slavini (Popov)
Paranannites aspenensis Hyatt and Smith
Juvenites sp. indet.
Anakashmirites angustecostatus (Welter)
Meekoceras gracilitatis White
Arctoceras mushbachanum (White)
Hemiprionites hungeri Kummel
Anasibirites kingianus (Waagen)

My new collections from the *Owenites* beds at Kotal-e-Tera contain four additional species which are described here. These are

Juvenites cf. *septentrionalis* Smith
Wyomingites aplanatus (White)
Hemiprionites typus (Waagen)
Wasatchites sp. indet.

Beds K5 and K6 contain a *Subcolumbites* fauna. Though bed K4 yielded no fossils it is lithologically more related to beds K5 and K6 than to the underlying units. The major part of the fossil collections was obtained from bed K6. This *Subcolumbites* fauna includes the following species:

Pseudosageceras multilobatum Noetling
Subvishnuites sp. indet.
Subvishnuites cf. *enveris* (Arthaber)
Xenoceltites sp. indet.
Procarnites kokeni (Arthaber)
Isculitoides cf. *originis* (Arthaber)
Subcolumbites perrinismithi (Arthaber)
Vickohlerites cf. *sundaicus* (Welter)
Meropella cf. *plejanae* Renz and Renz
Albanites triadicus (Arthaber)
Keyserlingites sp. indet.
Leiophyllites sp. indet.

Figure 3. Index map of localities where faunas of *Owenites* Zone age have been reported. (1) Lower limestone member of Thaynes Formation in southwestern Montana, southeastern Idaho, and northern Utah; (2) Thaynes Formation of northeastern Nevada and west-central Utah; (3) Moenkopi Formation of southwestern Utah; (4) Inyo Mountains, southern California; (5) northeastern Washington; (6) Sulphur Mountain beds of Alberta; (7) Needham Creek area, British Columbia; (8) Liard River area, British Columbia; (9) Ellesmere Island and Axel Heiberg Island; (10) Herlufsholm, Peary Land; (11) Spitsbergen; (12) Olenek-Lena River Basin, Siberia; (13) Okhotsk-Kolyma Land, Siberia; (14) Primorye Region around Vladivostok; (15) Iwai Formation of Kwanto Massif, Taho Formation of Shikoku, and Kamura Formation of Kyushu, Japan; (16) Malakoff Hill Group, Coal Creek, Wairakei Downs, South Island, New Zealand; (17) limestone with *Owenites* fauna, limestone with *Ophiceras crassecostatum*, and limestone with *Anasibirites multiformis*, Timor; (18) Gua Panjang fauna, Malaya; (19) *Owenites* beds of Kwangsi, China; (20) *Hedenstroemia* fauna of Himalayas in northern India, Kashmir, and Tibet; (21) upper Mittiwali Member of Mianwali Formation, Salt Range and Surghar Range, West Pakistan; (22) *Owenites* fauna of Kotal-e-Tera, Afghanistan; (23) *Owenites* fauna of northern Caucasus Mountains; (24) *Meekoceras* fauna of Yugoslavia; (25) Barabanja fauna of northeastern Madagascar.

Bed K7 is of Anisian age. Kummel and Erben (1968) have recorded the following ammonoids from this unit:

Beyrichites khanikofi (Oppel)
Discoptychites sp. indet.
Malletoptychites malletianus (Stoliczka)
Gymnites sp. indet.

The Triassic formations west of the Kabul-Gardez road crop out much more extensively than east of the road but are cut by numerous cross-faults. The sequence of units is the same as east of the road. The beds including the *Owenites* fauna are much more fossiliferous west of the road than they are on the east. However, the upper beds with the *Subcolumbites* are much less fossiliferous west of the road than they are to the east.

CORRELATION WITH REGIONS OUTSIDE OF AFGHANISTAN

Owenites Fauna

This is one of the most widespread and diverse of all Scythian faunas. The major localities of the world where faunas of this age are known are plotted on the map of Figure 3. A plot of the distribution of the genera represented in the *Owenites* fauna at Kotal-e-Tera is given on Table 1. The paper by Kummel and Erben (1968) contains a fairly detailed discussion and comparison of the Kotal-e-Tera *Owenites*

	Yugoslavia	Caucasus Mts.	Madagascar	Afghanistan	Salt Range, W. Pakistan	Kashmir	Spiti Region, Himalayas	Malaya	Timor (*Ophiceras* fauna)	Timor (*Owenites* fauna)	Timor (*Anasibirites* fauna)	New Zealand	China	Japan	Primorye Region	Siberia	Spitsbergen	Ellesmere Island	British Columbia	Western U.S.	Range of genus
Pseudosageceras	?	×	×	×	×	×	×	×	×				×		×		×	×		×	–
Subinyoites				×																	e
Subvishnuites		×		×						×		×	×								l
Xenodiscoides				×	×																×
Dieneroceras		×		×	?								×	×	×	×				×	l
Clypeoceras			×	×	×		×						×			?				×	×
Eoptychites			?	×	×		?														×
Owenites		×		×				×		×	×	×	×	×	×					×	×
Paranannites			×	×									×	×		×				×	×
Juvenites		×	×	×		×	×			×			×	×				×	×	×	×
Anakashmirites				×	×		×		×	×			×					×		×	l
Meekoceras	?			×	?		×						×		×	×		×		×	×
Arctoceras				×			×			×			×		×	×	×	×	×	×	×
Wyomingites		×		×								×					?			×	×
Hemiprionites				×	×									×		×	×			×	×
Wasatchites				×	×										×		×	×	×	×	×
Anasibirites				×	×		×				×		×	×	×	×				×	×

TABLE 1. GEOGRAPHIC DISTRIBUTION OF GENERA PRESENT IN THE *OWENITES* FAUNA AT KOTAL-E-TERA, AFGHANISTAN. SYMBOLS IN RIGHT HAND COLUMN AS FOLLOWS: ×, PRESENT ONLY AT THIS HORIZON; –, PRESENT IN BOTH YOUNGER AND OLDER HORIZONS; l, PRESENT ALSO IN LATER HORIZONS; e, PRESENT ALSO IN EARLIER HORIZONS.

fauna with faunas believed to be of the same age from other parts of the world. The new species added to the Kotal-e-Tera *Owenites* faunal collection (*Juvenites* cf. *septentrionalis*, *Wyomingites aplanatus*, *Hemiprionites typus*, and *Wasatchites* sp. indet.) further strengthen the conclusions arrived at earlier as to the affinities of this fauna. The species of *Juvenites* and *Wyomingites* are very common members of the *Meekoceras* fauna of western United States. *Hemiprionites typus* was originally described from the Upper Ceratite limestone of the Salt Range of West Pakistan (Waagen, 1895). This formation also yielded the type of *Anasibirites kingianus* (Waagen, 1895). *Wasatchites* is another, quite common, member of the so-called *Anasibirites* fauna.

In the Kummel and Erben (1968) paper on the Kotal-e-Tera collections, it was stated that there was complete mixing of the *Owenites* and *Anasibirites* faunas. One collection by H. K. Erben was made from the basal part of their gray limestone unit (collection A-3 in Kummel and Erben, 1968) and another from the rest of the unit (collection A-2). Both collections contain a so-called mixed fauna. During my own field investigation of the Kotal-e-Tera region I was not able to find any anasibiritid elements in my unit K2. Within my unit K3, mixing of the faunas was very evident.

Subcolumbites Fauna

The *Subcolumbites* fauna of Kotal-e-Tera comprises 12 species placed in 11 genera. The list of species in this fauna is given on page 488. The geographic distribution of the genera is shown on Table 2 and

	Albania (*Subcolumbites* fauna)	Chios (*Subcolumbites* fauna)	Mangyshlak Peninsula	Kotal-e-Tera, Afghanistan (*Subcolumbites* fauna)	Salt and Surghar ranges West Pakistan	Timor (*Prohungarites* fauna)	Kwangsi,China (*Subcolumbites* fauna)	Japan (*Subcolumbites* fauna)	Primorye Region (*Subcolumbites* fauna)	Olenek Region (*Olenekites* fauna)	Spitsbergen (*Keyserlingites* fauna)	Ellesmere Island (*Keyserlingites* fauna)	British Columbia (Toad-Grayling Formation)	Tobin Range (*Subcolumbites* fauna)	Confusion Range Utah	S.E. Idaho (*Prohungarites* fauna)	Range of genera
Pseudosageceras	×	×	×	×	×	×			×	×				×	×	×	e
Subvishnuites	×			×	×												e
Xenoceltites				×	×		×		×								e
Procarnites	×	×	×	×	×	×	×		×				×				×
Isculitoides	×	×		×	×	×	×		×				×	×		×	×
Subcolumbites	×	×		×		×	×	×	×					×			×
Vickohlerites		×		×													×
Meropella		×		×													×
Albanites	×	×	×	×		×											×
Keyserlingites				×						×	×	×	×	×		×	×
Leiophyllites	×	×	×	×			×		×				×				l

TABLE 2. GEOGRAPHIC DISTRIBUTION OF GENERA PRESENT IN THE *SUBCOLUMBITES* FAUNA AT KOTAL-E-TERA, AFGHANISTAN. SYMBOLS IN RIGHT HAND COLUMN AS FOLLOWS: ×, PRESENT ONLY AT THIS HORIZON; –, PRESENT IN BOTH YOUNGER AND OLDER HORIZONS; l, PRESENT ALSO IN LATER HORIZONS; e, PRESENT ALSO IN EARLIER HORIZONS.

the localities of late Scythian faunas are shown on the map of Figure 4. A number of the species in this fauna are prominent members of late Scythian faunas in several localities within Tethys from Albania to Timor. There is for instance *Albanites triadicus* (Arthaber), first described from the *Subcolumbites* fauna of Albania (Arthaber, 1908, 1911). In a comprehensive treatment of all late Scythian ammonoids, Kummel (1968b) has presented data to show that all of the many species of the genus *Albanites* that have been proposed are in reality synonyms of *Albanites triadicus*. In fact the genus *Albanites* is monotypic and confined to Tethys. In addition to its occurrence in the *Subcolumbites* fauna of Albania and at Kotal-e-Tera, Afghanistan, the species is present in the *Subcolumbites* fauna of Chios (Renz and Renz, 1948), the Mangyshlak Peninsula (Astakhova, 1960a, b) and the *Prohungarites* fauna of Timor. Another common and distinctive species of late Scythian age is *Pleuronilites hokeni*. It is present in late Scythian faunas of Albania, Chios, Mangyshlak Peninsula, Surghar Range in West Pakistan, Timor, and in Kwangsi, China. An equally widespread and distinctive species is *Subcolumbites perrinismithi* which is known from late Scythian faunas of Albania, Chios, Kwangsi and Japan. *Isculitoides originis* is now known from the late Scythian faunas of Albania, Chios, and Timor. It most probably is also present in the late Scythian fauna of the Narmia Member of the Mianwali Formation in the Salt Range and Surghar Range of West Pakistan. In regards to *Meropella*, this is the first record of a specimen of this genus outside of the *Subcolumbites* fauna of Chios. Species of *Xenoceltites, Subvishnuites*, and *Leiophyllites* are not common in the late Scythian. This is the first record of a late Scythian *Keyserlingites* from Tethys, though species of Anisian age are known from the Himalayas and Timor. Late Scythian species of *Keyserlingites* are known mainly from the circumarctic region and western North America.

Figure 4. Index map of localities where faunas of *Prohungarites* Zone age have been reported. (1) Upper Thaynes Formation, southeastern Idaho; (2) Upper Thaynes Formation, west-central Utah; (3) Tobin Formation, Tobin Range, Nevada; (4) *Subcolumbites* fauna Providence Range, southeastern California; (5) Humboldt Range, Nevada; (6) Toad-Grayling Formation, northeastern British Columbia; (7) upper Scythian of Ellesmere Island and Axel Heiberg Island; (8) Spitsbergen; (9) Olenek-Lena River Basin, Siberia; (10) Okhotsk-Kolyma Land, Siberia; (11) Primorye Region around Vladivostok; (12) Osawa Formation near Sendai, Japan; (13) south Otago, South Island, New Zealand; (14) *Prohungarites* fauna, Nifoekoko, Timor; (15) *Subcolumbites* fauna, Kwangsi, China; (16) *Prohungarites* fauna, Kashmir, Himalayas; (17) Narmia Member, Mianwali Formation, Salt Range and Surghar Range, West Pakistan; (18) *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan; (19) Tyur-Upa suite, Mangyshlak Peninsula, Caspian region; (20) *Subcolumbites* fauna of Chios; (21) *Subcolumbites* fauna of Albania; (22) *Tirolites* fauna of Campil Member of Werfen Formation.

SYSTEMATIC PALEONTOLOGY[1]

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Family SAGECERATIDAE Hyatt, 1900
Genus *PSEUDOSAGECERAS* Diener, 1895

Type species, *Pseudosageceras multilobatum* Noetling, 1905

Pseudosageceras multilobatum Noetling, 1905

A detailed synonymy of this species can be found in Kummel (1966). The *Subcolumbites* fauna at Kotal-e-Tera has yielded six fragmentary specimens; however, the distinctive character of the suture and conch shape makes recognition of the species comparatively easy. The *Owenites* fauna at Kotal-e-Tera has yielded a single specimen of this species. No other species of Scythian ammonoid is as long ranging or as widespread geographically. It is present in most ammonitiferous deposits of Scythian age.

Occurrence. *Owenites* fauna and *Subcolumbites* fauna at Kotal-e-Tera, Afghanistan.

Repository. MCZ 10166, 10173 (specimens from *Subcolumbites* fauna).

Family FLEMINGITIDAE Hyatt, 1900
Genus *SUBVISHNUITES* Spath, 1930

Type species, *Subvishnuites welteri* Spath, 1930 (= *Vishnuites* sp. Welter, 1922)

Subvishnuites sp. indet.

Plate 2, figure 14

Two small specimens of only fair preser-

[1] Abbreviations in this section are as follows: MCZ = Museum of Comparative Zoology; GPIBo = Geologisch-Paläontologisch Institut, Bonn; GSI = Geological Survey of India.

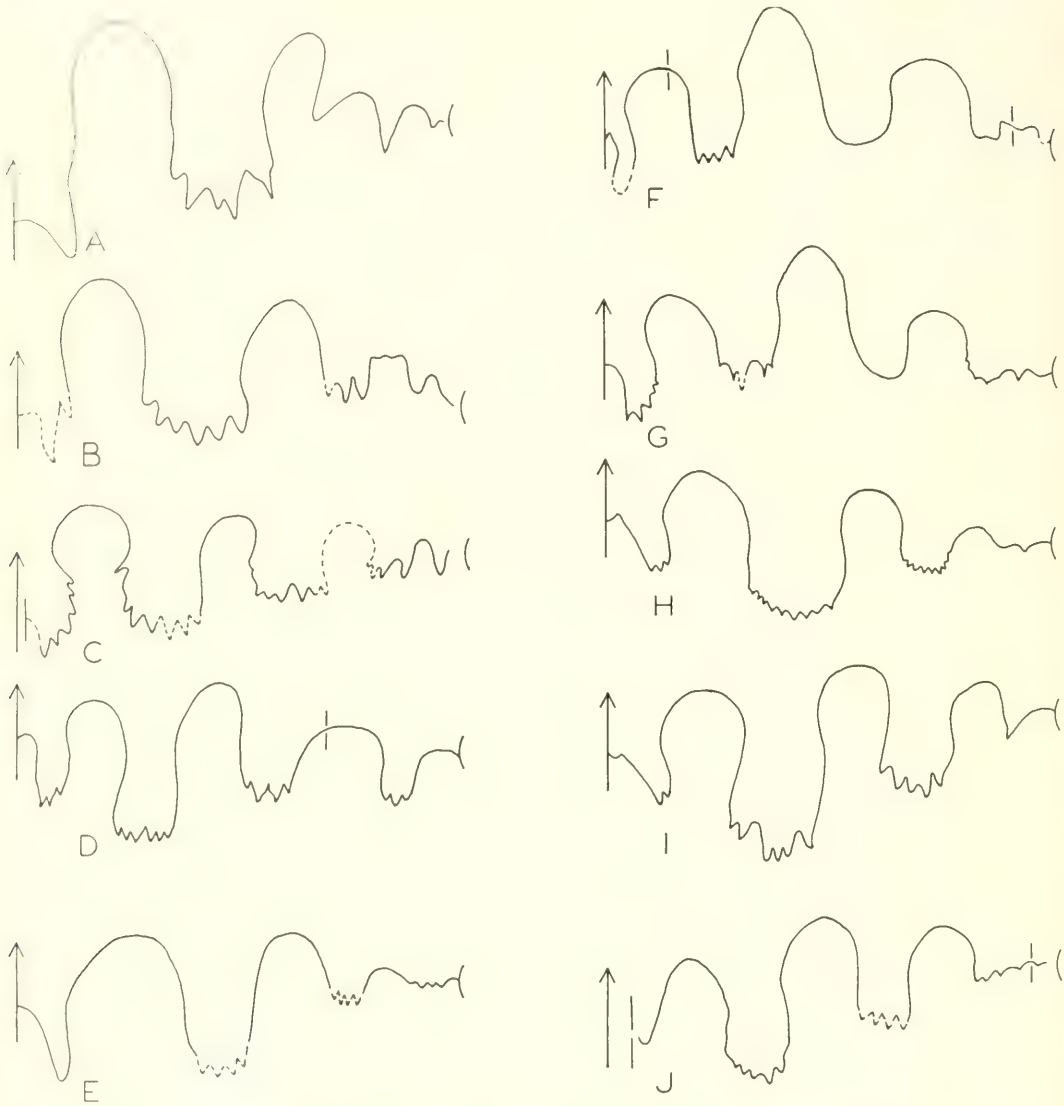

Figure 5. Diagrammatic representation of Scythian ammonoids from Kotal-e-Tera, Afghanistan. A, *Subcolumbites perrinismithi* (Arthaber) at a diameter of 14 mm, MCZ 10138; B, *Isculitoides* cf. *originis* (Arthaber) at a diameter of 16 mm, MCZ 10140; C, *Vickohlerites* cf. *sundaicus* (Welter) at a diameter of 20 mm, MCZ 10141; D, *Vickohlerites sundaicus* (Welter) at a diameter of 30 mm, holotype GPIBo 231; E, *Keyserlingites* sp. indet., at a diameter of 20 mm, MCZ 10143; F, *Albanites triadicus* (Arthaber) at a diameter of 45 mm, MCZ 10145; G, *Albanites triadicus* (Arthaber) at a diameter of 26 mm, from a weathered specimen, MCZ 10136; H, *Xenoceltites* sp. indet., at a diameter of 20 mm, MCZ 10137; I, *Leiophyllites* sp. indet., at a whorl height of 15 mm, MCZ 10151; J, *Wyomingites aplanatus* (White) at a diameter of 42 mm, MCZ 10163.

vation are in the collection. The distinctive features are the compressed, smooth, evolute conch, and the acute venter. The specimen which is illustrated has elliptical coiling and measures about 20 mm in diameter. The unfigured specimen has regular coiling and measures about 17 mm in diameter. The suture is not preserved on either of the specimens.

Most records of species of this genus are

based on few and generally poorly preserved specimens. The genus appears to be most common in the mid-Scythian *Owenites* Zone. The type species, *Subvishnuites welteri*, is from an *Owenites* fauna of Timor. It is now known from the same horizon in the Caucasus Mountains (described as *Parinyoites mastykensis* Popov, 1962), at Kotal-e-Tera, Afghanistan (Kummel and Erben, 1968), and from South Island, New Zealand (Kummel, 1959). The *Columbites* Zone contains a single Siberian species, described as *Inyoites eiekitensis* Popov (1962), which is quite similar to an indeterminate form in the *Columbites* fauna of southeast Idaho (Kummel, 1968b). The Narmia Member of the Mianwali Formation in the Surghar Range of West Pakistan contains poorly preserved and indeterminant species of *Subvishnuites* (Kummel, 1966). The horizon containing these specimens is of *Prohungarites* Zone age.

All the records to date on species of this genus, and especially on the specimens from the *Columbites* and *Prohungarites* zones, are woefully incomplete. The specimens all display smooth, compressed, evolute conchs, with acute venters. Any detailed analysis of this genus and its species will have to await the discovery of more abundant and better preserved specimens.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10150 (Pl. 2, fig. 14), MCZ 10147 (unfigured specimen).

Subvishnuites cf. *enveris* (Arthaber)

Plate 1, figures 8, 9

Xenaspis enveris Arthaber, 1911: 230, pl. 20(4), figs. 3a, b.

A single fairly well preserved specimen in the collection is very similar to the specimen from the *Subcolumbites* fauna of Albania assigned by Arthaber (1911) to *Xenaspis enveris*. It is unfortunate that Arthaber's type, and only specimen, of this species is apparently lost, because the illustration is a retouched photograph. I have personally examined and studied the remaining specimens studied by Arthaber (1908, 1911); the preservation, in hard, red limestone, often obscures shell features and the specimens are very difficult to prepare; this fact makes all of Arthaber's illustrations suspect.

My specimen measures 45 mm in diameter, approximately 20 mm for the width of the adoral whorl, 21 mm for the height, and 11.7 mm for the width of the umbilicus. The whorl sides are broadly arched, converging on to a rounded venter. The whorl sides bear widely spaced radial ribs that commence and are most conspicuous on the umbilical shoulder and decrease in intensity toward the venter which is smooth. The adoral half volution has four such ribs. The ribs are likewise present on the inner whorls as far as they are preserved. The umbilical shoulder is abruptly rounded and the umbilical wall, nearly vertical. Unfortunately, no trace of the suture is preserved on any part of the specimen.

Arthaber's specimen of *Xenaspis enveris* is slightly more evolute than my Afghan specimen (34 per cent versus 27 per cent) and has an acute venter on the adoral part of the living chamber. The ribbing, according to Arthaber, is developed only on the living chamber. The absence of ribs on the phragmocone could well be a matter of preservation. The suture of the Albanian specimen consists of two denticulated lateral lobes (Arthaber, 1911: pl. 20(4), fig. 3c).

It appears quite probable that the Albanian *Xenaspis enveris* is not conspecific with the Afghan specimen recorded here, though they are most probably congeneric; however, the assignment of these specimens to the genus *Subvishnuites* is open to question. The type species of *Subvishnuites* is based on a single specimen from the *Owenites* fauna of Timor. It is an evolute form with an acute venter, and with smooth lateral areas. Conspecific forms have been described by Kummel (1959: 443) from an *Owenites* fauna of South Island, New Zealand, by Popov (1962b: 42, as *Parinyoites*

yinyikensis from an *Owenites* fauna of the Caucasus Mountains, and by Kummel and Erben (1968) from the *Owenites* fauna of Kotal-e-Tera, Afghanistan. In addition the *Owenites* Zone of Kwangsi, China, contains *Subvishnuites tientungensis* Chao (1959). The specimen from the *Dieneroceras* Zone of Siberia (Popov, 1962a) described as *Inyoites eiekitensis* is a species of this genus. The *Columbites* Zone of southeast Idaho has yielded one fragmentary specimen that is quite similar to the Siberian S. *eiekitensis*. The Narmia Member of the Mianwali Formation in the Trans-Indus Surghar range of West Pakistan has yielded fragmentary specimens of this genus described as S. sp. indet. by Kummel (1966). These specimens are of late Scythian *Prohungerites* Zone age.

All of the species and specimens of the *Subvishnuites* mentioned above are smooth forms with acute venters. The Albanian *Xenaspis enveris* and the Afghan specimen recorded here have prominent radial ribs beginning on the umbilical shoulder and decreasing toward the venter. A case could be made that the Albanian and Afghan species are generically distinct from the more typical species of *Subvishnuites*. However, data are so incomplete on both the Albanian and Afghan specimens that it would be imprudent to establish a new genus with either of these specimens as type. Because of these factors and because there are no other late Scythian genera to which these specimens have any similarity, it seems best to assign them to *Subvishnuites*.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10148 (Pl. 1, figs. 8, 9).

Family XENOCELTITIDAE Spath, 1930

Genus *XENOCELTITES* Spath, 1930

Type species, *Xenoceltites subevolutus* Spath, 1930

Xenoceltites sp. indet.

Plate 2, figures 11–13

The genus *Xenoceltites* is very common and widely distributed in the mid-Scythian *Owenites* Zone. In the overlying *Columbites* Zone there is only one species, namely *X. spencei* (Smith, 1932). In the uppermost Scythian, *Prohungarites* Zone, there are only three recorded occurrences of species of this genus. There is first of all *Xenoceltites sinuatus* (Waagen) from the Narmia Member of the Mianwali Formation in the Salt Range of West Pakistan (Kummel, 1966). From Kwangsi, China, Chao (1959) has described *Xenoceltites crenoventrosus* from a *Subcolumbites* fauna. Finally, Kiparisova (1961) identified *X. spitsbergensis* from a *Subcolumbites* fauna in the Primorye Region. In all three of these reported occurrences, the species are established on very few specimens that in addition are only of poor to fair preservation.

The *Subcolumbites* fauna of Kotal-e-Tera has yielded three fragmentary specimens of fair preservation that clearly are xenoceltitids but which cannot be assigned with confidence to a particular species. The conch is moderately evolute with compressed whorls that are convergent to a narrowly rounded venter. The flanks bear forward-projecting constrictions. The suture is shown on Figure 5H. These Afghan specimens are quite similar to the fragmentary specimens Kummel (1966) has described from the Narmia Member of the Mianwali Formation in the Surghar Range of West Pakistan. *Xenoceltites sinuatus* (Waagen) from the same horizon in the adjacent Salt Range is known only from four fragmentary and generally poorly preserved specimens. These are all much larger than the specimen of *Xenoceltites* sp. indet. from the Surghar Range and the Afghan specimens recorded here, making direct comparison difficult and tenuous. The species from Kwangsi, China, *X. crenoventrosus* Chao (1959), is based on a single, fragmentary specimen of poor preservation. In this species the constrictions are very marked on the venter. The two specimens assigned by Kiparisova (1961) to *X. spitsbergensis* are quite similar to the

type of that species from the *Owenites* Zone of Spitsbergen. In this species the whorls are more rounded and the constrictions broader and more widely spaced.

The genus *Xenoceltites* is thus now known from late Scythian faunas at four localities, but each record leaves much to be desired, and comparisons are very difficult.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10137 (Pl. 2, fig. 11), MCZ 10157 (Pl. 2, figs. 12, 13), MCZ 10169 (unfigured specimen).

Family PROPTYCHITIDAE Waagen, 1895

Genus *PROCARNITES* Arthaber, 1911

Type species, *Parapopanoceras kokeni* Arthaber, 1908

Procarnites kokeni (Arthaber) 1908

Plate 1, figure 16

Parapopanoceras kokeni Arthaber, 1908: 259, pl. 11(1), figs. 1a–c, 2a, b.

Hedenstroemia sp. Arthaber, 1908: 284, pl. 3, fig. 2.

Procarnites kokeni (Arthaber), 1911: 215, pl. 17(1), figs. 16, 17, pl. 18(2), figs. 1–5; Diener, 1915: 228; Diener, 1917: 167; C. Renz, 1928: 155; Spath, 1934: 181, fig. 55; Renz and Renz, 1947: 61; Renz and Renz, 1948: 81; pl. 8, figs. 5, 6–6a, 7–7a, 8–8a, 9–9a, pl. 9, figs. 2–2a; Kummel, *in* Arkell et al., 1957: L138, fig. 171, 4; Kummel, 1966: 390, pl. 2, figs. 10–13.

Procarnites kokeni var. *evoluta* Renz and Renz, 1947: 61; Renz and Renz, 1948: 82, pl. 9, figs. 1–1a.

Procarnites kokeni var. *panteleimonensis* Renz and Renz, 1947: 61, 78; Renz and Renz, 1948: 82, pl. 8, figs. 3–3a, pl. 9, figs. 3–3a.

Procarnites acutus Spath, 1934: 183, pl. 5, figs. 4a, b (= *Hedenstroemia* sp. Arthaber, 1908: 284, pl. 3, fig. 2); Chao, 1959: 89, 255, pl. 32, figs. 8, 9, pl. 33, figs. 1–8.

Procarnites skanderbegis Arthaber, 1911: 216, pl. 18(2), figs. 6, 7; Diener, 1915: 229; C. Renz, 1928: 155; Spath, 1934: 182; Renz and Renz, 1947: 61; Renz and Renz, 1948: 82, pl. 8, figs. 4–4a.

Procarnites andrusovi Kiparisova, 1947 (Bajarunas, 1936, *nom. nud.*): 132, pl. 28, figs. 2–4, text-figs. 11–13; Astakhova, 1960b: 149.

Procarnites oxynostus Chao, 1959: 88, 254, pl. 32, figs. 1–7, 10–12, text-figs. 28a–d.

This is another, rather common and distinctive species in late Scythian faunas of Tethys and closely related regions. My collections from the *Subcolumbites* fauna of Kotal-e-Tera contain two specimens of rather poor preservation. The distinctness of the conch shape and suture of this species makes identification easy. The specimen which is illustrated on Plate 1, figure 16 has a diameter of 51 mm and an umbilical diameter of 9 mm. The second specimen is not quite as well preserved but does show the suture which, though weathered, is clearly that of this species.

A complete analysis of all species of *Procarnites* can be found in Kummel (1968b). The long synonymy reflects a great deal of misconception regarding this species. Examination of Arthaber's (1908, 1911) original types from Albania and the large collection of this species from Chios, studied by Renz and Renz, has given a clearer perspective to the nature of variation in this species. On the basis of this analysis it can readily be established that within Tethys there is only a single species of *Procarnites*, namely *Procarnites kokeni*. This species is also known from Kwangsi, China (Chao, 1959), where, however, another unique species of this genus is also present, namely the specimen described as *Digitophyllites suni* (Chao, 1950, 1959). *Megaphyllites immaturus* Kiparisova (1947) from the Primorye Region and *Procarnites modestus* Tozer (1965) from British Columbia I believe to be one and the same species, differing from *P. kokeni* in the presence of constrictions.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10154 (Pl. 1, fig. 16), MCZ 10155, 10171 (unfigured specimens).

Family PARANANNITIDAE Spath, 1930

Genus *JUVENITES* Smith, 1927

Type species, *Juvenites kraffti* Smith, 1927

Juvenites cf. *septentrionalis* Smith, 1932

Plate 3, figure 1

Juvenites septentrionalis Smith, 1932: 110, pl. 31,

figs. 31–40; Kummel and Steele, 1962: 687, pl. 159, figs. 1–11.

Juvenites sanctorum Smith, 1932: 110, pl. 31, figs. 22–30.

Nannites sinuosus Kiparisova, 1947: 141, pl. 28, figs. 6–8.

Nannites sinuosus var. *pressula* Kiparisova, 1947: 141, fig. 27.

This species is one of the more common and distinctive forms in the *Owenites* Zone of western United States. My collections from the *Owenites* fauna at Kotal-e-Tera, Afghanistan, contain a single, slightly crushed individual that does not show a suture. However, the uniqueness of the conch shape and pattern of ribbing is such that there is every reason to believe it is very closely related to *J. septentrionalis* if not conspecific with it. Kummel and Steele (1962) have given data on the range of intraspecific variation that is present in at least one population of this species. On the basis of these data I fail to see the distinctness of *Nannites sinuosus* Kiparisova (1947) from an *Owenites* fauna in the Caucasus Mountains. There is some similarity between *J. septentrionalis* and the Himalayan *J. herberti* (Diener), *J. hindostanus* (Diener), and *J. medius* Krafft and Diener. Evaluation of the differences among these species is difficult since the Himalayan species were based on only one or two specimens per species. Similar forms have been described from the beds with *Owenites egrediens* in Timor by Welter (1922).

Occurrence. *Owenites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10162 (Pl. 3, fig. 1).

Genus *ISCULITOIDES* Spath, 1930

Type species, *Isculites originis* Arthaber, 1911

Isculitoides cf. *originis* (Arthaber)

Plate 1, figures 12–15

Isculites originis Arthaber, 1911: 259, pl. 23(7), figs. 1–10; Diener, 1915: 157; C. Renz, 1928: 155; Kutassy, 1933: 540; Renz and Renz, 1947: 60; Renz and Renz, 1948: 33, pl. 13, figs. 7–7a, 9–9a, 11–11b, 12–12b, pl. 14, figs. 6–6a, 9–9a.

Isculitoides originis,—Spath, 1934: 198, pl. 14, figs. 2a–d, text-figs. 59b, c.

Isculites globulus Renz and Renz, 1947: 60, 74; Renz and Renz, 1948: 34, pl. 34, figs. 4–4a, 5–5a, 8–8b, 10–10c, 11–11b.

Isculites antiglobulus Renz and Renz, 1947: 60, 74; Renz and Renz, 1948: 35, pl. 13, figs. 1–1a, 10–10a, pl. 13, figs. 2–2a, 3–3a, 5–5a, 8–8a.

Isculites globulus-originis Renz and Renz, 1947: 60, Renz and Renz, 1948: 35, pl. 13, figs. 6–6a, pl. 14, figs. 1–1a, 2–2a, 3–3a.

Isculites globulus-antiglobulus Renz and Renz, 1947: 60; Renz and Renz, 1948: 35, pl. 13, figs. 4–4a, pl. 14, figs. 7–7a.

Two incomplete, but fairly well preserved, specimens in the collection are closely allied but most probably not conspecific with *Isculitoides originis*. The conch is highly involute and with depressed whorls. The lateral areas and the venter are broadly rounded. The umbilical shoulder is subangular and the umbilical wall nearly vertical. The suture is shown on Figure 5B.

Isculitoides originis is one of the most common species in the *Subcolumbites* fauna of Chios. A complete restudy of the very large collection assembled by Renz and Renz has been undertaken by Kummel (1968b). In that review are included the documentation and discussion to show that this species displays a large degree of variation in width of the conch and in size of the umbilicus. In the Chios population of *Isculitoides originis*, the umbilical shoulder is always well rounded, even in the more depressed forms, in contrast to the subangular umbilical shoulder of the specimens recorded here. Among the known species of *Isculitoides*, only *originis* from Chios is known from a large number of specimens. The same species is also quite abundant in the *Subcolumbites* fauna of Albania, where Arthaber (1911) records 54 specimens in his collections. This same species (*originis*) is also known from Nifoekoko, Timor (Spath, 1934: 198). The genus *Isculitoides* is represented in the Narmia Formation, in the Salt Range of West Pakistan (Kummel, 1966). However,

because of poor preservation the specific affinity of these Pakistan specimens cannot be determined. The late Scythian fauna of Kwangsi, China, contains *Isculitoides ellipticus* Chao (1959). This appears to be a more compressed form. The late Scythian of the Primorye Region contains *Isculitoides suboviformis* Kiparisova (1954, 1961). This species has a highly depressed whorl section but is otherwise quite like the Afghan specimens recorded here. The upper Thaynes formation of southeast Idaho contains a species of *Isculitoides* that is quite like the specimens described here (Kummel, 1968b). The Tobin Formation of Nevada also contains a new species of *Isculitoides* but this is quite different from the Afghan forms (Kummel, 1968b). Finally *Isculitoides minor* Tozer (1965) from British Columbia is quite similar to the Kwangsi *I. ellipticus* and the forms from the Thaynes Formation of southeast Idaho. Small globular ammonoids, as *Isculitoides*, are very difficult forms to study. Few large populations of *Isculitoides* are known; most species of this genus are known from small and often poorly preserved samples; at the same time, however, the genus is represented in most late Scythian faunas and in some of these it is a dominant form.

Occurrence. *Subcolumbites* fauna at Kotal-e-Tera, Afghanistan.

Repository. MCZ 10140 (Pl. 1, figs. 14, 15), MCZ 10149 (Pl. 1, figs. 12, 13), MCZ 10167 (unfigured specimen).

Genus *SUBCOLUMBITES* Spath, 1930

Type species, *Columbites perrinismithi* Arthaber, 1908

Subcolumbites perrinismithi (Arthaber)

Plate 1, figures 1–3

Columbites perrinismithi Arthaber, 1908: pl. 12, fig. 1; Arthaber, 1911: 262, pl. 23(7), figs. 19, 20; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 20, pl. 11, figs. 7–7a.

Subcolumbites perrinismithi,—Spath, 1930: 77; Spath, 1934: 203, pl. 12, figs. 5a, b; Kummel, *in* Arkell et al., 1957: 140, figs. 172, 15a, b.

Columbites europaeus Arthaber, 1908: 278, pl. 12, fig. 2; Arthaber, 1911: 261, pl. 23(7), figs. 13–18; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 19, pl. 11, figs. 3–3a, 4–4a, 5–5a, 6–6a.

Subcolumbites europaeus,—Spath, 1934: 204, pl. 12, figs. 6a, b, text-fig. 62c.

Columbites europaeus perrinismithi Renz and Renz, 1947: 59; Renz and Renz, 1948: 20, pl. 11, figs. 1–1b, 2–2b.

Columbites mirditensis Arthaber, 1911: 263, pl. 24(8), figs. 2, 3, 4; Diener, 1915: 112; C. Renz, 1928: 155; Renz and Renz, 1947: 59; Renz and Renz, 1948: 21.

Subcolumbites mirditensis,—Spath, 1934: 205.

Subcolumbites kwangsianus Chao, 1959: 128, 304, pl. 30, figs. 14–17, text-fig. 41c.

Columbites asymmetricus Chao, 1959: 127, 303, pl. 30, figs. 10–13.

Subcolumbites cf. *perrinismithi*,—Bando, 1964: 99, pl. 3, figs. 18, 19, pl. 4, fig. 3.

This very distinctive species is represented in the collection by two fragmentary specimens. The larger of the specimens (Pl. 1, fig. 1) shows the typical fine, forwardly projecting ribbing of the species. On the smaller specimen the ribbing is only faintly developed but this appears to be due mainly to preservation. The smaller specimen has a diameter of 15 mm, and at that stage the venter is broadly rounded. Due to faulty preservation one can't be sure if the venter of the larger specimen sharpens, at least a little, as in some of the specimens of this species from Albania and Chios. The suture (Fig. 5A) is visible on the smaller of the specimens and is quite typical for the species.

This species is a common member of latest Scythian faunas from Albania, Chios, Kwangsi, and Japan. The synonymy given above reflects the multiplicity of names that have been introduced for this species. Restudy of all the critical type collections, except those from China, clearly shows the real relationship of all these forms. A thorough discussion of this species is given in Kummel (1968b).

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10138 (Pl. 1, figs. 2, 3), MCZ 10146 (Pl. 1, fig. 1).

Genus *VICKOHLERITES* Kummel, 1968

Type species, *Prenkites sundaicus* Welter, 1922

Vickohlerites cf. *sundaicus* (Welter)

Plate 1, figure 4

Prenkites sundaicus Welter, 1922: 150, pl. 168 (14), figs. 18–21; Kutassy, 1933: 621; C. Renz, 1945: 301; Renz and Renz, 1947: 60; Renz and Renz, 1948: 29, pl. 12, fig. 1; Chao, 1959: 306.

"*Prenkites*" *sundaicus*.—Spath, 1930: 77; Spath, 1934: 188, 209.

Vickohlerites sundaicus,—Kummel, 1968a: 9, pl. 1, figs. 6, 7.

A single, incomplete specimen in the collection is allied to the specimen from Timor assigned to *Prenkites sundaicus* by Welter (1922) and which Kummel (1968a) selected as the type of his new genus *Vickohlerites*. The specimen on hand has a diameter of approximately 43 mm. The venter on the inner whorls, at a diameter of approximately 20 mm, is distinctly flattened with rounded ventral and umbilical shoulders. The maximum width of the whorl is at the midline of the lateral areas. On the following volution, at a diameter of approximately 25 mm, the venter is arched but the cross section of the whorls is still much broader than high. At the maximum diameter of the specimen the venter is more highly arched and the width and breath of the whorls more equal in dimensions. At this diameter also the maximum width is at the umbilical shoulder.

The type specimen of *Prenkites sundaicus* from Timor has depressed whorls at all stages, though the degree of depression decreased adorally. Likewise, throughout the ontogeny of the Timor specimen the maximum width is at the umbilical shoulder. Also the umbilical shoulder is acutely rounded in all growth stages.

The suture on the Afghan specimen is reproduced on Figure 5C. The first lateral lobe is entirely on the venter, the second lateral lobe is on the lateral area and the auxiliary lobe is on the umbilical wall. The suture of the holotype of *Vickohlerites sundaicus* is reproduced on Figure 5D. The number of elements in these two sutures is the same but the shape of the saddles and lobes and the pattern of denticulation are quite different. This raises a question as to whether this Afghan specimen is even generically allied to the type of *Vickohlerites sundaicus* from Timor. There is a degree of similarity in the pattern of the suture of this Afghan specimen to the suture of *Zenoites* represented in the *Subcolumbites* fauna of Chios. *Zenoites*, however, is a genus characterized by strong constrictions and these are not present on my Afghan specimen. Likewise, the suture of the Afghan specimen is similar to that of *Chioceras*, another unique genus of the *Subcolumbites* fauna of Chios. Here again though, there is a striking difference in conch morphology, as *Chioceras* has a prominent ventral keel.

Critical comparison of the Afghan and Timor forms is difficult as each is represented by a single specimen. There is an overall similarity between the two specimens, but intriguing differences in whorl shape and suture. The specimens are surely specifically distinct and perhaps even generically. However, the Afghan specimen is too poorly preserved to be selected as the type of a new species and genus. The identification given here reflects its closest affinities based on the data available.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10141 (Pl. 1, fig. 4).

Genus *MEROPELLA* Renz and Renz, 1947

Type species, *Arianites* (*Meropella*) *plejanae* Renz and Renz, 1947

Meropella cf. *plejanae* Renz and Renz

Plate 1, figures 10, 11

Arianites (*Meropella*) *plejanae* Renz and Renz, 1947: 67, 79; Renz and Renz, 1948: 95, pl. 3, figs. 3–3b, 11–11b.

Meropella plejanae,—Kummel, *in* Arkell et al., 1957: L140, fig. 172, 12.

This genus and species had previously been known only from a few specimens in

the *Subcolumbites* fauna of Chios. The specimen recorded here is incomplete and somewhat poorly preserved. The diameter is 18 mm, width of adoral whorl about 9 mm, height about 4 mm and the umbilical diameter is approximately 10 mm. The whorls are depressed, with a broadly arched venter and narrow, rounded, lateral areas. This Afghan specimen differs from the Chios forms in its highly depressed whorls. In the Chios specimens the width and height of the whorls are approximately equal. The suture is only vaguely discernible on my specimen. On the ventral region one can see a narrow lanceolate ventral lobe, adjoined by a phylloid first lateral saddle and then the first lateral lobe. A second lateral lobe straddles the ventral shoulder, and a small auxiliary lobe is vaguely indicated on the umbilical wall. The base of the lobes are not observable so the nature of the denticulation, if any, is not known. The Chios *M. plejanae* has this same general suture pattern.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10142 (Pl. 1, figs. 10, 11).

Family MEEKOCERATIDAE Waagen, 1895

Genus *WYOMINGITES* Hyatt, 1900

Type species, *Meekoceras aplanatum* White, 1880

Wyomingites aplanatus (White)

Plate 3, figures 12–14

Meekoceras aplanatum White, 1879: 112; 1880: 112, pl. 31, figs. 1a, b, d (not c); Smith, 1904: 373, pl. 41, figs. 4–6; Hyatt and Smith, 1905: 146, pl. 11, figs. 1–14, pl. 64, figs. 17–22, pl. 77, figs. 1, 2.

Meekoceras (Gyronites) aplanatum,—Diener, 1915: 196.

Xenodiscus aplanatus,—Mojsisovics, 1886: 75.

Xenaspis ? aplanata,—Waagen, 1895: 290.

Ophiceras aplanatum,—Frech, 1902: 631; 1908, pl. 61, fig. 1.

Flemingites aplanatus,—Smith, 1932: 51, 52, pl. 11, figs. 1–14, pl. 22, figs. 1–23, pl. 39, figs. 1, 2, pl. 64, figs. 17–32.

Wyomingites aplanatus,—Hyatt, 1900: 556; Spath, 1934: 250, 251, fig. 84; Kummel, 1954: 185; Kummel, *in* Arkell et al., 1957: L142, figs. 175, 7a–c.

Wyomingites cf. *aplanatus*,—Kummel, 1959: 444, figs. 5, 6; Kummel and Steele, 1962: 696, pl. 99, figs. 3, 4.

My collections from the *Owenites* Zone at Kotal-e-Tera contain five, more or less fragmentary, specimens of only fair preservation of this species. The largest specimen has a diameter of approximately 65 mm. The species is comprised of forms with compressed, evolute conchs and flattened venter; the whorl sides are only slightly arched. The suture is shown on Figure 5J.

This species was first described on the basis of specimens from the *Meekoceras* limestone of southeast Idaho, and is quite common in the *Owenites* Zone of western United States. The Afghan specimens recorded here agree in all essential features to the specimens from western United States. Though I have fairly extensive collections of this species from the *Meekoceras* limestone of southeast Idaho, most specimens are too incomplete to yield significant measurements. I can, however, match my Afghan specimens to those from Idaho with no difficulty. The suture also is essentially the same except for what appears to be a more highly developed auxiliary series on the umbilical shoulder and wall. It is, however, quite similar to the suture reproduced by Smith (1932: pl. 22, fig. 3) for a specimen of this species from southeast Idaho. My own collections of this species from southeast Idaho show that there is considerable variability in the shape, length, and pattern of denticulation of the auxiliary lobe. In summary, I can observe no significant differences between these Afghan specimens and those of *W. aplanatus* from western United States. I would also include here the fragmentary specimen from the small *Owenites* fauna of South Island, New Zealand (Kummel, 1959). In addition it is highly possible that the specimen from the *Arctoceras* fauna of Spitsbergen, assigned by Stolley (1911: 123, pl. 9, fig. 5)

to *Meekoceras (Gyronites) aplanatum* White, is correctly identified. Spath (1934: 251) considered this identification wrong and suggested that these forms should be referable to *Svalbardiceras* Frebold. This change in generic assignment was strongly influenced by his belief that the *Arctoceras* fauna of Spitsbergen was late Scythian in age. Kummel (1961) has presented arguments to establish that the *Arctoceras* fauna of Spitsbergen is of mid-Scythian, *Owenites* Zone, age.

Occurrence. *Owenites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10161 (Pl. 3, fig. 13), MCZ 10163 (Pl. 3, fig. 14), MCZ 10164 (Pl. 3, fig. 12), MCZ 10172 (unfigured specimens).

Family NORITIDAE Karpinsky, 1889

Genus *ALBANITES* Arthaber, 1909

Type species, *Pronorites triadicus* Arthaber, 1908

Albanites triadicus (Arthaber)

Plate 2, figures 1–9

Pronorites triadicus Arthaber, 1908: 264, pl. 11, figs. 4a–c; Arthaber, 1911: 204, pl. 17(1), figs. 8, 9; Diener, 1915: 231; C. Renz, 1928: 155; Kutassy, 1933: 624; Renz and Renz, 1947: 61; Renz and Renz, 1948: 84, pl. 14, figs. 14–14b.

Albanites triadicus,—Spath, 1934: 275, fig. 95.

Pronorites osmanicus Arthaber, 1911: 205, pl. 17(1), fig. 10; Diener, 1915: 231; C. Renz, 1928: 155.

Albanites osmanicus,—Spath, 1934: 276.

Pronorites cf. *osmanicus*,—Renz and Renz, 1947: 62; Renz and Renz, 1948: 86, pl. 15, figs. 6–6c.

Pronorites arbanus Arthaber, 1911: 205, pl. 17(1), figs. 11, 12; Diener, 1915: 230; Welter, 1922: 94, pl. 155, figs. 10–14; C. Renz, 1928: 255; Kutassy, 1933: 624; C. Renz, 1945: 301; Renz and Renz, 1947: 61; Renz and Renz, 1948: 85, pl. 14, figs. 13–13b, 15–15b, pl. 15, figs. 5–5c.

Albanites arbanus,—Spath, 1934: 277.

Pronorites arbanus var. *mediterranea* Renz and Renz, 1947: 62; Renz and Renz, 1948: 85, pl. 14, figs. 12–12b.

Pronorites spec. ind. ex aff. *arbani*,—Welter, 1922: 95, pl. 155(1), fig. 9.

Svalbardiceras ovalis Kiparisova, 1947: 164, pl. 39, figs. 3, 4, text-figs. 60, 61.

Pronorites arbanus var. *sundaica* Renz and Renz, 1948: 85.

Albanites welteri Spath, 1934: 278.

Pronorites orientalis Renz and Renz, 1947: 62; Renz and Renz, 1948: 86, pl. 15, figs. 2–2b.

Pronorites shaubi Renz and Renz, 1947: 62, 78; Renz and Renz, 1948: 87, pl. 15, figs. 4–4a.

Pronorites shaubi var. *timorensis* Renz and Renz, 1948: 87.

Pronorites shaubi var. *kephalovunensis* Renz and Renz, 1947: 62, 78; Renz and Renz, 1948: 87, pl. 15, figs. 3–3a.

Pronorites reicheli Renz and Renz, 1947: 62, 79; Renz and Renz, 1948: 88, pl. 15, figs. 1–1c.

Albanites danispanensis (Astakhova) 1960a: 143, pl. 34, figs. 4, 5; Astakhova, 1960b: 150.

Aspidites hasserti Arthaber, 1911: 249, pl. 21(5), fig. 16; Spath, 1934: 275.

Meekoceras (Koninckites) hasserti,—Diener, 1915: 198.

Dagnoceras komanum Arthaber, 1911: 242, pl. 21(5), fig. 11; Diener, 1915: 115; Smith, 1932: 65; Spath, 1934: 269, 275.

Pseudosibirites cfr. *dichotomus* Waagen, Arthaber, 1911: 254, pl. 22(6), fig. 8.

Anasibirites cfr. *dichotomus*,—Arthaber, 1911: 273.

Sibirites cf. *dichotomus*,—Diener, 1915: 255.

This species, though never occurring in any great abundance, is present in most of the late Scythian faunas known from Tethys. Justification and discussions of the long synonymy of this species is given in Kummel (1968b). There have been seven species and four variety names introduced for this group. Aside from extremely narrow conceptions of species, poor preservation and preparation of specimens accounts for at least some of the multiplicity of names. The *Subcolumbites* fauna of Kotal-e-Tera has yielded six specimens of this species, five of which are illustrated on Plate 2, figures 1–9. The sutures from two of the specimens are shown on Figures 5F, G. The smallest of these specimens has a diameter of 21 mm and the largest a diameter of approximately 47 mm. All the specimens are phragmocones. The flattened venter with distinct cross ridges is a conspicuous feature of this species. One specimen (Pl. 2, figs. 8, 9) has slightly more rounded ventral shoulders. This, however, is a variation that can readily be seen in the larger Albanian and Chios populations

of this species. None of the specimens preserve a perfect suture due to factors of weathering and the nature of the preservation. However, even though details are obscured, the suture (Figs. 5F, G) is identical to that for other members of this species.

As now understood, *Albanites triadicus* is the only species of the genus *Albanites* and is confined to Tethys. This species is present in the *Subcolumbites* fauna of Albania and Chios, in the *Columbites* Zone of Astakhova (1960a, b) on the Mangyshlak Peninsula, the *Subcolumbites* fauna of Kotal-e-Tera, Afghanistan, and in the *Prohungarites* fauna of Timor.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10136 (Pl. 2, figs. 6, 7), MCZ 10145 (Pl. 2, fig. 1), MCZ 10152 (Pl. 2, figs. 8, 9), MCZ 10153 (Pl. 2, figs. 4, 5), MCZ 10156 (Pl. 2, figs. 2, 3), MCZ 10168 (unfigured specimens).

Family PRIONITIDAE Hyatt, 1900

Genus *HEMIPRIONITES* Spath, 1929

Type species, *Goniodiscus typus* Waagen, 1895

Hemiprionites typus (Waagen)

Plate 3, figures 2–9

Goniodiscus typus Waagen, 1895: 128, pl. 9, figs. 7–10; Diener, 1915: 135; Mathews, 1929: 31, pl. 5, figs. 5–21.

Hemiprionites typus,—Spath, 1929: 270; Spath, 1934: 330, fig. 114; Kummel, *in* Arkell, et al., 1957: L144, fig. 177, 3.

This species is represented by a single well preserved specimen of approximately 55 mm in diameter. The species is characterized by a highly compressed involute conch and a tabulate venter.

The types of this species consist of four, mainly fragmentary, poorly preserved specimens from the Upper Ceratite limestone of the Salt Range in West Pakistan. This is the upper part of the Mittiwali Member of the Mianwali Formation of Kummel (1966). The lectotype (Waagen, 1895: pl. 9, figs. 8a–c; Pl. 3, figs. 2, 3 of this report) is a very poorly preserved phragmocone that consists of only a portion of the venter and one side of the conch. The specimen measures about 29.0 mm in diameter, 11.0 mm for the width of the adoral whorl, 15.7 mm for the height, and 5.4 mm for the diameter of the umbilicus. The poor preservation makes highly doubtful the presence of the cross ridges on the venter as in Waagen's reconstruction of this specimen. Only parts of the suture are visible and these are highly weathered. The three remaining paralectotypes are equally poor specimens. The suture illustrated by Waagen (1895: pl. 9, fig. 9) was taken from a small fragment of whorl section (Pl. 3, fig. 8) that is also weathered. The illustration of the smallest of Waagen's specimens (1895: pl. 9, fig. 10; Pl. 3, figs. 6, 7 of this report) is highly inaccurate. There are no serrations on the ventral shoulders and the lateral ornament is nothing more than very faint growth lines. Finally, the illustration reproduced by Waagen (1895: pl. 9, fig. 7; Pl. 3, fig. 9 of this report) of the largest of his specimens bears little resemblance to the actual specimen.

The basic form of the conch of my Afghan specimen is essentially the same as that of the type specimens of Waagen from the Salt Range of West Pakistan. The suture on the Afghan specimen is not clearly visible, but there appears to be some difference, in the shape of the saddles, with the suture of Waagen's paralectotype. My own extensive collections from the Upper Ceratite limestone, and especially from Chhidru where Waagen collected his specimens of *H. typus*, contain a fair number of specimens of this species, though the preservation is not much better than that of Waagen's material. However, within this collection, variability in the shape of the lobes and saddles is quite evident. Though both the Salt Range and Afghan specimens are poorly preserved, I have no doubt but they are conspecific.

Kummel and Erben (1968) described an-

other species of *Hemiprionites*, *H. hungeri*, from the *Owenites* beds at Kotal-e-Tera. This species is very distinct in the larger size of the umbilicus and transverse ribs on the truncated venter. *Hemiprionites timorensis* Spath (1934: 331) from the *Anasibirites* beds of Timor is very nearly allied to the type species, as are the American species of *Hemiprionites* described by Mathews (1929) and the Spitsbergen species described by Spath (1934). There is a distinct possibility that all these forms are conspecific; however, because of the poor preservation and incompleteness of data on the Tethyan specimens, it seems best to keep them distinct for the time being.

Occurrence. *Owenites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10159 (Pl. 3, figs. 4, 5).

Family SIBIRITIDAE Mojsisovics, 1896

Genus *WASATCHITES* Mathews, 1929

Type species, *Wasatchites perrini* Mathews, 1929

Wasatchites sp. indet.

Plate 3, figures 10, 11

This species is represented in the collection by two specimens of fair to poor preservation. The better of the two specimens, illustrated in Plate 3, figures 10, 11, has a diameter of 30.5 mm. The distinguishing features of the genus are clearly evident. These are: the compressed conch, with convergent whorl sides, and a low arched venter; prominent umbilical nodes from which radiate two ribs that decrease in size toward the venter. The suture is not preserved.

The genus *Wasatchites* is a conspicuous member of the so-called "*Anasibirites*" fauna and is characteristic of the *Anasibirites* Subzone of the *Owenites* Zone. All of the numerous species of this genus look very much alike. The type species is based on specimens from the *Anasibirites* fauna of Fort Douglas, Utah (Mathews, 1929). My Afghan specimen is very similar to the type species and could very well be conspecific with it. However, better preserved specimens are needed to establish this relationship with any degree of certainty. Species of this genus have been described from British Columbia (McLearn, 1945), Axel Heiberg Island (Tozer, 1961) and Spitsbergen (Spath, 1934). In each of these areas the genus occurs within the mid-Scythian *Owenites* Zone. The genus is also present in the Upper Ceratite limestone of the Salt Range, West Pakistan.

Occurrence. *Owenites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10158 (Pl. 3, figs. 10, 11), MCZ 10160 (unfigured specimen).

Genus *KEYSERLINGITES* Hyatt, 1900

Type species, *Ceratites subrobustus* Mojsisovics, 1885

Keyserlingites sp. indet.

Plate 1, figures 5–7

A small specimen of 22 mm in diameter is our first record of the genus *Keyserlingites* in late Scythian strata of Tethys. The specimen appears to be all phragmocone and has a whorl height of 9 mm and an umbilical diameter of 7.5 mm. The whorl sides are slightly convex and converge toward a broadly rounded venter. The umbilical shoulder is abruptly rounded and the umbilical wall nearly vertical. There are large nodes, one approximately every quarter volution, that are anchored on the umbilical shoulder and extend upward on the flanks. The most adoral node, at a diameter of 21 mm, extends half way across the lateral areas. The suture consists of a simple pronged ventral lobe, a large first lateral saddle and first lateral lobe, and much smaller second lateral saddle and lobe; low, denticulated auxiliary lobe occupies the umbilical wall (Fig. 5E). Two small specimens of only fair preservation are believed to be even younger stages of this species. The specimen illustrated on Plate 1, figures 6, 7 has faint indication of the umbilical nodes and a suture with the basic pattern of that of the larger specimen.

The general shape of the conch, the nodes, and the suture identify this specimen as *Keyserlingites*. The specimen is most probably a juvenile form. On the basis of studies on several well preserved specimens of *Keyserlingites subrobustus* from British Columbia and Ellesmere Island, Tozer (1965) has been able to clarify the relations between *Keyserlingites* and *Durgaites*. Tozer's suggestion, however, that the Himalayan "*Durgaites*" *dieneri* and the Timor "*D.*" *angustecostatus* may be late Scythian in age, rather than Anisian, as concluded by Diener (1907, 1912), Spath (1934) and Welter (1915), is rejected. The full aspect of this problem has been discussed by Kummel (1968b). *Keyserlingites* is known mainly from the circum-Arctic region where two species are present in late Scythian strata. One of these species, *Keyserlingites subrobustus* Mojsisovics, is present in northern Siberia, Spitsbergen, Ellesmere Island, and in British Columbia. A second species, *Keyserlingites middendorffi* (Keyserling) is known only from northern Siberia. The *Prohungarites* fauna of the Thaynes Formation of southeast Idaho contains two species of *Keyserlingites*, and the underlying *Columbites* fauna a single species. Zakharov (personal communication) reports the occurrence of another new species of this genus in late Scythian strata of the Primorye Region.

Occurrence. *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10139 (Pl. 1, figs. 6, 7), MCZ 10143 (Pl. 1, fig. 5), MCZ 10144 (unfigured specimen).

Family USSURITIDAE Hyatt, 1900

Genus *LEIOPHYLLITES* Diener, 1915

Type species, *Monophyllites suessi* Mojsisovics, 1882

Leiophyllites sp. indet.

Plate 2, figure 10

This identification is based on a single, loose, weathered, incomplete specimen lying on the strata of the *Prohungarites* Zone. The topography of the outcrop and matrix of the specimen support the contention that the specimen is from the *Prohungarites* Zone. The specimen consists of little more than a quarter of a complete conch and is all phragmocone. The inner whorls are highly weathered, the outer whorl to a much lesser extent. The evolute nature of the conch and compressed whorls is clearly evident. These features of the conch plus the suture (Fig. 5I) establish at least the generic affinity of the form.

The genus *Leiophyllites* is represented in the *Subcolumbites* fauna of Albania and Chios, in the *Stacheites* Zone of Astakhova (1960a) on the Mangyshlak Peninsula, in the *Subcolumbites* faunas of Kwangsi, China, and in the Primorye Region. It is also apparently present in late Scythian strata of British Columbia (Tozer, 1965).

Occurrence. Loose specimen, presumably from *Prohungarites* Zone, Kotal-e-Tera, Afghanistan.

Repository. MCZ 10151 (Pl. 2, fig. 10).

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(Received 7 November 1967.)

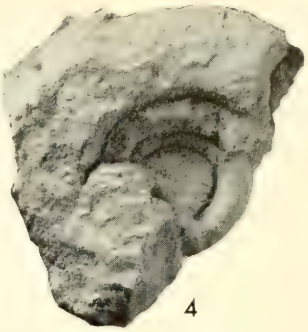
PLATE 1. SUBCOLUMBITES, VICKOHLERITES, KEYSERLINGITES, SUBVISHNUITES, MEROPELLA, ISCULITOIDES, PROCARNITES

Figure		*Page*
1–3	*Subcolumbites perrinismithi* (Arthaber) 1, MCZ 10146, × 2; 2, 3, MCZ 10138, × 2.	495
4	*Vickohlerites* cf. *sundaicus* (Welter) MCZ 10141, × 1.	496
5–7	*Keyserlingites* sp. indet. 5, MCZ 10143, × 1.5; 6, 7, MCZ 10139, × 2.	500
8, 9	*Subvishnuites* cf. *enveris* (Arthaber) MCZ 10148, × 1.	491
10, 11	*Meropella* cf. *plejanae* Renz and Renz MCZ 10142, × 2.	496
12–15	*Isculitoides* cf. *originis* (Arthaber) 12, 13, MCZ 10149, × 2; 14, 15, MCZ 10140, × 2.	494
16	*Procarnites kokeni* (Arthaber) MCZ 10154, × 1.	493

All specimens from *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

1

2



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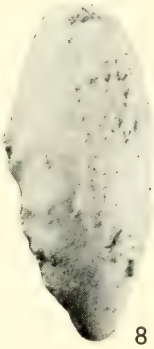

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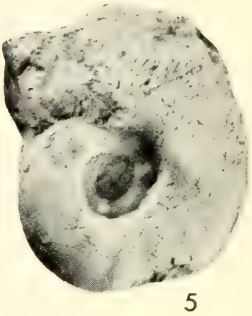

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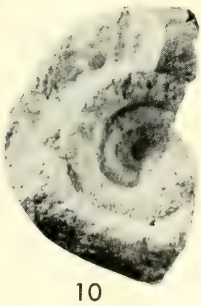

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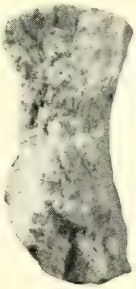

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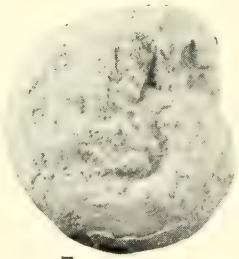

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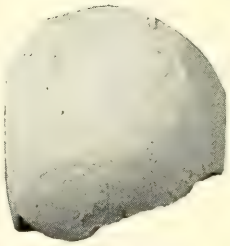

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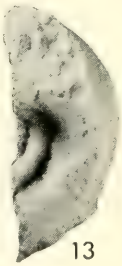

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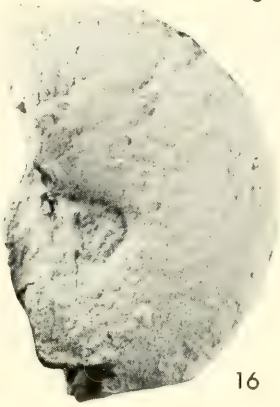

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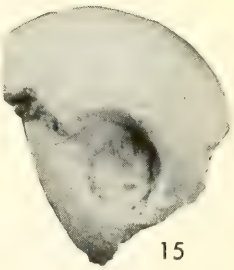

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PLATE 2. ALBANITES, LEIOPHYLLITES, XENOCELTITES AND SUBVISHNUITES

Figures		*Page*
1–9	*Albanites triadicus* (Arthaber). 1, MCZ 10145, × 1; 2, 3, MCZ 10156, × 2; 4, 5, MCZ 10153, × 2; 6, 7, MCZ 10136, × 1.5; 8, 9, MCZ 10152, × 2.	498
10	*Leiophyllites* sp. indet. MCZ 10151, × 1.	501
11–13	*Xenoceltites* sp. indet. 11, MCZ 10137, × 1.5; 12, 13, MCZ 10157, × 2.	492
14	*Subvishnuites* sp. indet. MCZ 10150, × 2.	489

All specimens from *Subcolumbites* fauna, Kotal-e-Tera, Afghanistan.

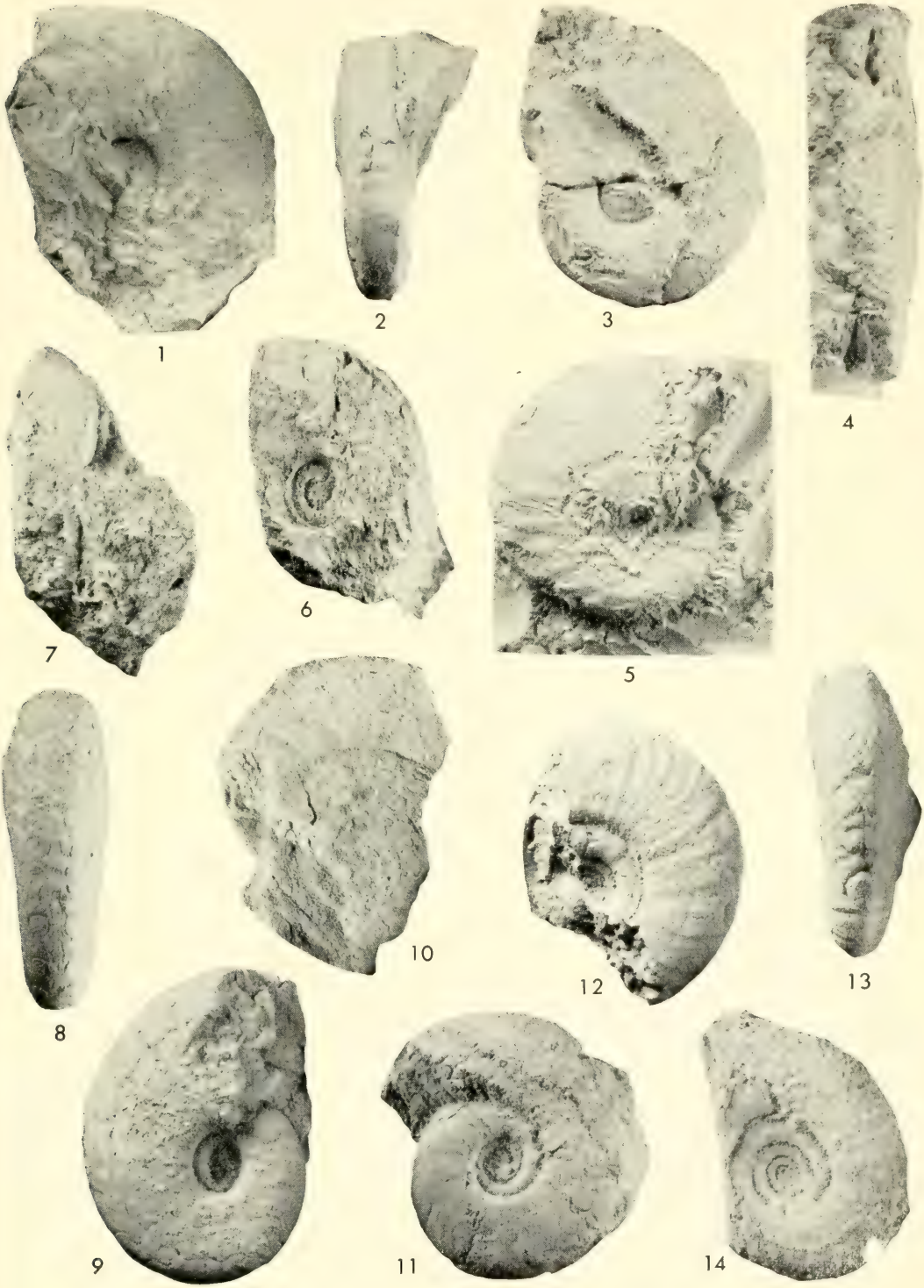
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PLATE 3. JUVENITES, HEMIPRIONITES, WASATCHITES, AND WYOMINGITES

Figures		Page
1	*Juvenites* cf. *septentrionalis* Smith. From *Owenites* Zone, Kotal-e-Tera, Afghanistan. MCZ 10162, × 2.	493
2, 3	*Hemiprionites typus* (Waagen). From Upper Ceratite limestone at Chhidru, Salt Range, West Pakistan. Lectotype of Waagen (1895, pl. 9, fig. 8) GSI 7104, × 1.5.	499
4, 5	*Hemiprionites typus* (Waagen). From *Owenites* Zone, Kotal-e-Tera, Afghanistan. MCZ 10159, × 1.	499
6, 7	*Hemiprionites typus* (Waagen). From Upper Ceratite limestone at Chhidru, Salt Range, West Pakistan. Paralectotype of Waagen (1895, pl. 9, fig. 10) GSI 7106, × 1.5.	499
8	*Hemiprionites typus* (Waagen). From Upper Ceratite limestone at Chhidru, Salt Range, West Pakistan. Paralectotype of Waagen (1895, pl. 9, fig. 9) GSI 7105, × 1.	499
9	*Hemiprionites typus* (Waagen). From Upper Ceratite limestone at Chhidru, Salt Range, West Pakistan. Paralectotype of Waagen (1895, pl. 9, fig. 7) GSI 7103, × 1.	499
10, 11	*Wasatchites* sp. indet. From *Owenites* Zone, Kotal-e-Tera, Afghanistan. Ventral and lateral views, MCZ 10158, × 1.5.	500
12–14	*Wyomingites aplanatus* (White). From *Owenites* Zone, Kotal-e-Tera, Afghanistan. Lateral view of three specimens: 12, MCZ 10164; 13, MCZ 10161; 14, MCZ 10163, × 1.	497

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